ECOLOGICAL MONOGRAPHS

VOL. 18 JULY, 1948 NO. 3

OFFICIAL PUBLICATION OF THE ECOLOGICAL SOCIETY OF AMERICA

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PUBLISHED QUARTERLY BY DUKE UNIVERSITY PRESS
DURHAM, N. C., U. S. A.

ECOLOGICAL MONOGRAPHS

A QUARTERLY JOURNAL
FOR ALL PHASES OF BIOLOGY

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Agents in Great Britain: The Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1. Prices can be had on application.

Entered as second-class matter December 18, 1930, at the Post Office at Durham, North Carolina, under the Act of Congress of March 3, 1879.

CATASTROPHIC MASS MORTALITY OF MARINE ANIMALS AND COINCIDENT PHYTOPLANKTON BLOOM ON THE WEST COAST OF FLORIDA, NOVEMBER 1946 TO AUGUST 1947*

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CATASTROPHIC MASS MORTALITY OF MARINE ANIMALS AND COINCIDENT PHYTOPLANKTON BLOOM ON THE WEST COAST OF FLORIDA, NOVEMBER 1946 TO AUGUST 1947

INTRODUCTION

Discoloration of sea water caused by bloom or swarming of phytoplankton is a commonly reported phenomenon, although one far from well understood. The discoloration may or may not be accompanied by mortality ranging from the death of a few animals and species in a restricted area to mass mortality of catastrophic proportions. Instances of plankton blooms accompanied by mortality have been related by Whitelegge (1891), Torrey (1902), Gilchrist (1914), Hornell (1917), Sommer & Clark (1946), and Gunter, Smith & Williams (1947). The last is a preliminary notice to this paper. The phenomenon seems to be world-wide and the above accounts related to India, Africa, Europe, Florida, California, Australia and Japan. Otterstrom & Steeman (1940) describe a dinoflagellate bloom which caused death of fishes in fresh water.

Nishikawa (1901), Kofoid (1911), Taylor (1917 a.b.), Lund (1935), McKernan & Scheffer (1942), and Brongersma-Sanders (1943), have given accounts indicating that phytoplankton blooms were the cause of mortality of marine organisms. Records of sea water discoloration without notice of accompanying mortality are very numerous, and to quote them would be superfluous.

Mortality of fishes and other marine animals on the lower west coast of Florida has been reported by Jefferson, Porter & Moore (1878), Jefferson (1878), Pierce (1883, 1884), and Taylor (1917, 1917 a). Taylor gave as the most probable explanations of the mortality the release of occluded bottom gases by small seismic disturbances or the presence of abnormally large numbers of "Peridinii." The phenomenon is a recurrent one (Taylor 1917) and has been reported in the same region in 1844, 1854, 1878, 1880, 1882, 1883, 1908, and 1916. The next occurrence was in the fall of 1946. Thus there were nine cases in one hundred and two years that occurred on an average of every eleven years but irregularly spaced from one to thirty years apart.

Members of the staff of the Marine Laboratory of the University of Miami made certain observations throughout the 1946-1947 sequence of outbreaks. They are less complete than is desirable but in view of the absence of other sources of detailed information on this subject, it seems worthwhile to set them forth in some detail. The majority of field trips and observations were made and samples taken by Gunter. Chemical determinations were carried out by Williams and the plankton samples analyzed by Davis. The causative organism was tentatively identified originally by Smith, under whose direction the investigation was conducted. Samples of plankton and reports on the results of investigations in progress were made available to the United States Fish and Wildlife Service and have been referred to in their mimeographed reports.

The authors are much indebted to Mr. Jay N. Darling, of Captiva Island, to the Coloosahatchee Conservation Club, especially to the President, Mr. E. W. Smith, to Mr. Fred Smoot, of Fort Myers, and Mr. J. N. Thompson, of Key West, all of whom were liberal in providing facilities for this investigation.

TIME AND AREA COVERED BY THE MORTALITY

Mackerel fishermen first noticed dead and dying fishes and turtles in streaks of discolored water ten to fourteen miles offshore from Naples on November 20, 1946. (See Figure 1.) The mortality moved northward and shoreward and reached the bays behind Sanibel and Captiva Islands, as far north as Boca Grande Pass. Fish continued dying there until late in January 1947. During the first days of February fish drifted ashore on Englewood beach. This was the most northerly record of the mortality. The fish may have drifted to Englewood from the Boca Grande region. According to all reports, no mass mortality occurred north of Pine Island Sound. However, during the middle of January, commercial fishermen reported catching "sick" cobia, ***Rachycentron canadus*** (Linnaeus), in a net ten miles off Pass a Grille beach. Due to their condition the fish were released. This area is off the mouth of Tampa Bay. Sick fish are not common in marine waters and it is more reasonable than not to suspect that the conditions that caused the fish to be sick off Pass a Grille beach were the same as those that killed large numbers of fishes further south.

To the southward the mortality of marine animals was definitely reported as far as Cape Romano. On January 19th the captain of a small freighter from Panama reported that he sailed through dead fishes from Dry Tortugus to Fort Myers. If this report is accepted, it means that the disturbance was many

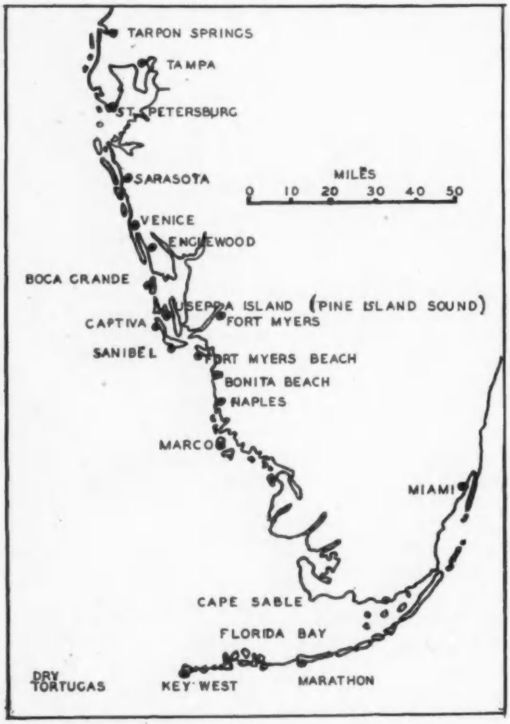

FIG. 1. Catastrophic mass mortality. South Florida.

miles farther offshore at the southern end of the Florida Peninsula than at its northern limit.

After the end of January 1947, there were no further accounts of the death of fishes and other animals until April 2nd when reports, then several days old, were received that the surface of the ocean from Cape Florida to Marathon and west almost to Key West was covered with dead fishes of all kinds. This area covers most of the outer waters of Florida Bay, the water lying between the keys and the southern tip of the peninsula. Later fish mortality was reported south of the keys in some places but apparently it had disappeared by the end of April.

On June 20th fish were noted dying again at Bonita beach, south of Fort Myers and within the next three days the mortality had spread northward again to Fort Myers beach and the area around Captiva Island. The mortality continued on into early July when it died out again only to break out once more near Venice on July 18th, whence it moved north to Sarasota and the beaches north of St. Petersburg during July and August.

Note In brief, the observed mortality of fishes and other marine animals ranged from Sarasota to the Florida Keys, and covered a distance of one hundred and fifty miles and an area of a few thousand square miles, and extended in time from the latter half of November 1946 to the latter half of August 1947, a period of about eight months. Possibly both the duration and the area were a little more extensive than the report indicates on account of the incompleteness of observations and possible lack of reports from certain areas.

MORTALITY OF MARINE ANIMALS

Verbal and newspaper accounts of the mortality were quite common. Certain of these will be summarized before firsthand observations are given. A few turtles were seen dead and dying by mackerel fishermen from Naples, Florida. A small number of "porpoises," the bottlenose dolphin, *Tursiops truncatus* (Montague), were reported dead in the Fort Myers region.

All kinds of animals were killed, the chief invertebrates noted being barnacles (Balanus), and oysters *(Ostrea virginica),* on pilings; coquinas (Donax), which were washed up on the beaches in small windrows in some places; penaeid shrimp (Penaeus), and crabs of various kinds, of which the common blue crab *(Callinectes sapidus)* was the most common. Mr. Jay N. Darling, of Captiva Island, wrote on January 26, 1947:

> Shrimp have been coming in on the Gulf side where we never saw them before, either dead or alive. They are extra large shrimp and in one little cove where they were concentrated there were several bushels of them dead. I have never seen such large shrimp in these waters.

Presumably they were *Penaeus setiferus,* the common commercial shrimp of the Gulf and South Atlantic Coasts, but they could have been *P. aztecus.*

Doubtless large numbers of invertebrates were killed, but they did not readily float and the numbers seen were small compared to the vast hordes of fishes floating in the waters and washed up on the beaches.

According to common report the dead fishes consisted chiefly of "bottom fish" and large numbers of mullet, with very few mackerel, pompano or sharks killed. Mr. J. C. Galloway of Punta Gorda, wrote on February 13th that he had examined the fishes at Englewood beach, which were dried by that time, and found about twenty-five species. He mentioned snake eels, *Ophicthus gomesii,* blue angelfish, *Angelichthys ciliaris,* and shortnosed batfish, *Ogcocephalus radiatus.*

In the Florida Bay region during the last of March, the dead fishes floating were reported to be chiefly "bottom fish" such as grunts, groupers, yellowtail, etc., with no mackerel, kings or bonita seen.

Many mullet were reported killed. Fishermen and other observers stated in several instances that schools of mullet entering the discolored water died immediately. On January 26, 1947, Mr. Darling wrote:

> Migrating fish, mostly mullet, coming in from the Gulf through Blind Pass are dying by the hundreds as soon as they get into the infested water today. It would appear that most all the fish in the bay waters are already dead and on Friday, with a N.E. wind, were deposited in great numbers on the east shore of Captiva Island.

FIG. 2. Heavy accumulation of dead fish on surface of ocean seen from airplane near entrance to Tampa Bay, July 1947. The mass of floating fish marks the edge of the oily red water. *(Photograph: Courtesy of Associated Press.)*

At Captiva, grunts, *Haemulon plumieri,* floated ashore first. Then in the last days of December a long line of pinfish, *Lagodon rhomboides,* floated ashore. Good pictures of this line or "drift" of floating fish were furnished by Mr. Darling. The fish were floating so closely together they were touching. The width of the strip of fish was two to three yards wide and extended as far as the eye could see. According to Darling, it was miles long. Later other fishes drifted in to the Captiva Island shore. Grunts and pinfish were reported to have come ashore first in all localities.

The amount of fishes killed was enormous. One home owner on Captiva Island buried 60,000 fishes from two hundred feet of Bay beach. The same area had to be cleaned on three other occasions. An airplane pilot flying over Florida Bay reported that "the surface of the ocean was covered with dead fish." In the preliminary note, Gunter, Smith, and Williams (1947) very conservatively estimated that 50,000,000 fishes were killed. Since that time the area increased and a recheck of the area and the numbers of fishes seen floating and washed ashore leads to the corrected estimate that the fishes killed must have numbered in the nighborhood of a half billion.

On January 16, 1947, Fort Myers beach was examined. There was a windrow of dead fish, somewhat dried, high up on the beach. This windrow was approximately ten yards wide, varying in width up and down the beach, and the fish were touching or piled on top of one another. Counts were made and it was estimated that the fishes varied from one hundred and fifty to one hundred and seventy to a foot of shoreline. Grunts and pinfish made up the vast majority, but other species were present. On account of the condition of the fish, counts of species were not made. A smaller thin line of fish, more recently dead and more heterogeneous so far as species were concerned, lay lower down on the beach near the water's edge. According to reports this line of dead fish extended thirty miles. We did not see more than a few miles of it.

All of the fish in the neighborhood of residences were cleaned off the beach and buried by local authorities. Twenty-four hours later a fresh group had

been stranded up and down the beach. Table 1 gives the numbers and species found in a ten-yard stretch of the beach on January 17th. Table 2 shows the additional species seen in one hundred and fifty yards of the beach. The fish listed in the original ten yards of beach were not counted in the one hundred and fifty-yard stretch.

TABLE 1. The numbers and species of fishes dead on a ten-yard stretch of the Fort Myers beach on January 18, 1947. These fishes washed in during a 24-hour period.

Signalosa mexicana	55	Myrophis punctatus	2
Lagodon rhomboides	37	Mugil cephalus	2
Galeichthys felis	13	Menticirrhus americanus	2
Hyporhamphus unifasciatus	10	Strongylura marina	1
Achirus fasciatus	10	Gymnothorax moringa (?)	1
Eucinostomus gula	9	Peprilus paru	1
Chloroscombrus chrysurus	6	Caranx hippos	1
Opsanus tau	6	Oligoplites saurus	1
Brevoortia patronus	5	Leiostomus xanthurus	1
Bairdiella chrysura	5	Menticirrhus littoralis	1
Gymnothorax vicinus (?)	5	Prionotus scitulus	1
Harengula pensacolae	4	Ogcocephalus vespertilio	1
Ophichthus sp.	4		

TABLE 2. The numbers of fishes seen in 150 yards of Fort Myers beach in addition to those species, the more common ones, counted in 10 yards of beach as given in Table 1 are listed.

Pogonias cromis	5	Chaetodipterus faber	1
Scomberomorus maculatus	4	Nautopaedium porossisimum	1
Elops saurus	2	Balistes vetula	1
Bagre marina	1	Monocanthus hispidus	1
Synodus foetens	1	Spheroides maculatus	1
Caranx chrysos	1	S. testudineus	1
Archosargus probatocephalus	1	Chilomycterus schoepfi	1
Cynoscion nebulosus	1	Symphurus plagiusa	1

In addition to the fishes stranded on the Fort Myers beach, thousands of fishes floated on the water out to a distance of twelve nautical miles offshore. Up to four or five miles offshore they were very thick and in some places were touching each other. The average distribution seemed to be about one to a square yard of surface. Farther out the floating fishes became thinner and at ten miles offshore were distributed about one to the acre. Counts of species were not made.

At various places around Captiva Island on January 28th, *Cynoscion nebulosus, Centropomus undecimalis, Sphyraena barracuda,* and *Sciaenops ocellata* were seen in addition to the other fishes reported. On the same day large tarpon, *Tarpon atlanticus*, and jewfish, *Garrupa nigrita*, up to four hundred pounds in weight were seen offshore between Boca Grande Pass and Captiva Pass.

On April 12th, an examination of the waters of Florida Bay N.E. of Key West was made. The heavy concentrations of dead fishes had been scattered by high winds and heavy seas during the three previous days. The fishes were distributed about one or two to the acre over a very large area, the extent of which was not covered during several hours journey in a boat. Table 3 gives the numbers of species captured by a dipnet while cruising in a commercial mackerel boat at about ten knots.

TABLE 3. Dead and dying fishes picked up by a dip net in Florida Bay, N.E. of Key West, on April 12, while cruising in a commercial mackerel boat.

Haemulon sciurus	39	Monocanthus hispidus	4
H. parra	12	Mugil cephalus	2
Pomacanthus aureus	7	Eques pulcher	2
Galeichthys felis	6	Opsanus tau	2
Lactophrys quadricornis	4	Mycteroperca bonaci	1

On June 25 following the second mortality of fishes in the Fort Myers area the beach at Bonita was examined. There were about seventeen fish to ten yards of beach. The toadfish (Opsanus), the soles (Achirus) and spiny puffers (Chilomycterus) were most abundant. Later examination by boat in waters offshore showed a line of fish along a tide-rip, made up mostly of the same species, with a great predominance of toadfish. The only large fish seen was a snook, *Centropomus undecimalis* (Bloch). Many lady crabs, *Hepatus epheliticus* (Linnaeus) and horseshoe crabs were also seen floating in the tide-rip. From the air on the same day scattered dead fish were seen floating from just north of Naples to Captiva Island, a distance of about thirty miles. This second occurrence of mortality within the same area was not nearly so heavy as the first episode, probably because the population of fishes had been materially reduced by the first mass mortality.

It is worthwhile to call attention to the relative abundance of the species of fishes of southwest Florida as indicated by those found dead on the beaches. Evidence has been given in a series of papers, summarized and cited in Gunter (1945), that the Sciaenidae, Engraulidae, Otolithidae, Clupeidae, Mugilidae and Ariidae are the families of fishes of greatest abundance on the Texas and Louisiana coasts. Unpublished data collected by W. W. Anderson on the Georgia coast show that the croakers (Sciaenidae) predominate in trawl catches there as they do in Louisiana and Texas. Along the South Atlantic and Gulf coasts of the United States the fish fauna is similar, but along both coasts of Florida there is a break or transition where the fauna turns tropical and West Indian. This problem has never been studied specifically, but the correctness of the statement is shown by general observation. The data on the fishes killed during the mortality under discussion gives additional evidence and is worth consideration in that light. Table 4 gives the most abundant families of fishes in order of their rank, as well as it could be established from the estimates of dead fishes washed up on the beaches of the lower West Florida coast. Large numbers of mullet were also reported

killed, but not many were seen by us. The table indicates a relative abundance differing from that of Texas and Louisiana as shown by Gunter (1945) and it appears that southward along the Florida coast the Haemulidae, Sparidae, Hemirhamphidae, Gerridae and other fish families become increasingly important while the Sciaenidae and Otolithidae decrease in numbers.

TABLE 4. The most abundant families of fishes found dead on the lower West Florida beaches in January, 1947, in order of their abundance.

1. Haemulidae	5. Hemirhamphidae
2. Sparidae	6. Achiridae
3. Clupeidae	7. Gerridae
4. Ariidae	8. Sciaenidae

DISCOLORATION OF THE WATER

The writers did not observe the various discolorations of the water in the sequence in which they developed, although all phases were noticed at one time or another. However, there was a definite sequence. First the water became turbid or slightly changed in appearance from a clear green or bluish-green to a more opaque green. As fisherman described it the water did not "look right." Then it became yellowish green and later greenish-yellow. At the next stage, and possibly only in spots a few yards or a few hundred yards across, the water became a bright saffron yellow in color. Dr. O. E. White, of the Blandy Experimental Farm, while flying over Florida Bay on the regular commercial flight from Havana to Miami, observed that the water was dotted with small patches of yellow water. Gunter and Smith observed a patch of this water in Pine Island Sound one mile south of Useppa Island on January 28, 1947. The water color was very striking and peculiar in contrast to the green waters of the bay. The water had other peculiar characteristics in addition to color. It was viscid like a thin oil and a bucket of it taken up as a sample had an oily appearance. It felt very slimy, although it was not ropy, and ran off the hands and fingers in thin gelatinous-like streams. The yellow water probably did not develop in all places where mortality occurred and the accentuated yellow color was not a necessary predecessor of the mortality of the larger organisms.

After the yellow color stage the water turned brown slowly and then "red," the color which in the popular mind was associated with the mortality of fishes. This red water, which varied with the direction of the light from which it was viewed, appeared to be an opaque, dull, dark amber with a greenish yellow cast. At other times it seemed to have a faint lavender tint. After the dark brown or red stage the water reverted to an opaque green or greenish blue color, characteristically the color of waters with heavy plankton growth.

PLANKTON CONTENT OF THE WATER

A number of samples of the plankton were obtained. Those from the lower west coast region were taken not only from areas in which mortality was still taking place, but also from where the condition had reverted more or less to normal as indicated by lack of discoloration of the water, fish no longer dying, and resumption of activities by the mackerel fishermen. In the Key West region, plankton samples were obtained at two localities near Key West, one in an area where fish mortality was occurring and one where there was no evidence of such mortality, although in the latter locality the water was somewhat discolored. Mr. Darling of Captiva Island is responsible for collecting certain samples of the plankton, which otherwise could not have been obtained.

DESCRIPTION OF COLLECTIONS AND METHODS OF ANALYSIS

Samples of unconcentrated, preserved sea water were obtained by Darling as follows: one sample on January 24th, three hundred yards offshore on the Gulf side of Captiva Island (in yellow water), a second sample at the same location twenty-four hours later, as well as samples on the latter date three quarters mile east of Captiva Pass in Pine Island Sound, five miles off Captiva Pass in the Gulf and two miles off Redfish Pass in the Gulf. An unconcentrated sample of the yellowish water was obtained by the authors on January 18th in Matanzas Pass near the dock northwest of Fort Myers beach. Much brighter yellow water was found later elsewhere, but no unconcentrated samples of this were obtained. In the Key West area, unconcentrated samples were obtained from three and one-half miles off Content Keys and two miles off Barracuda Key. In addition an unconcentrated sample was obtained in brownish-yellow water in the Gulf two hundred yards south of Redfish Pass on Captiva Island on June 25.

All other samples were net samples. Those from the Fort Myers area were non-quantitative and taken

TABLE 5. List of net plankton samples obtained. See test for fuller explanation.

Plankton Sample Number	Corresponding Chemical Sample	Date	Location
1	D	January 18	In cut near dock in Matanzas Pass, northwest of Fort Myers Beach.
2	A	January 18	300 yards southwest of Fort Myers Beach.
3	–	January 18	½ mile southwest of Fort Myers Beach.
4	O	January 19	Gordon Pass, near Naples.
5	M	January 19	1 mile off Gordon Pass.
6	K	January 19	3 miles off Gordon Pass.
7	–	January 21	Mouth of Blind Pass, Captiva Island.
8	–	January 21	Strand Dock, Roosevelt Pass, Captiva Island.
9	–	January 21	Upper end, Roosevelt Pass, Captiva Island.
10	–	January 21	Clam Bay, Captiva Island.
11	F	January 28	1 mile southeast of Useppa Island.
12	–	January 28	Mouth of Boca Grande Pass.
13	Q	April 12	2-½ miles north of Content Keys.
14	R	April 12	2 miles north of Barracuda Key.
15	S	June 25	½ mile off Big Hickory Pass, Bonita Beach.
16	T	June 25	Estero Bay, Florida.

with net of No. 20 mesh. Samples from the Key West area were taken with Clarke-Bumpus nets of No. 20 mesh. The data on net samples are shown in Table 5.

Of the net samples, numbers 1, 7, 10, 11 and 13 were in greenish yellow or bright yellow water. Fish were seen dying in Clam Bay (Sample Number 10), south of Useppa Island (Sample Number 11), and off Content Keys (Sample Number 13). The samples from off Fort Myers beach (Samples Number 2 and 3) were from water that showed a reddish-brown discoloration. The samples near Naples (Numbers 4, 5 and 6), were in an area previously affected, but which had recovered. They were turbid green or blue. The remaining samples were taken for the purposes of comparison.

Immediate examination in the field was made of the January net samples from the Fort Myers area, and these preliminary examinations were the basis of the statements on the plankton by Gunter, Smith, & Williams (1947).

In analysis, the unconcentrated samples were concentrated somewhat by decanting a measured amount of supernatant water from the thoroughly settled sample. All organisms in one drop of the remaining water were then counted after shaking and simple calculations were made to estimate the number of organisms per liter of the original sea water sample.

The non-quantitative net samples from the Fort Myers area were analyzed by counting the first two or three hundred organisms encountered in a few drops of the thoroughly mixed sample. Results were expressed as percentage of total organisms. In addition, because this method does not necessarily indicate the importance of an organism in the plankton (large number of small organisms do not represent as much organic material as small numbers of large organisms), rough estimates were made to determine what organisms formed the bulk of the two.

The quantitative net samples from the Key West area were analyzed as follows: all the organisms in one drop of the sample were counted so as to determine both relative and absolute numbers of the smaller organisms. Then all the larger organisms in one cubic centimeter were counted. For purposes of comparison with the Fort Myers area samples, calculations of percentages were made from these results.

GENERAL RESULTS

The abundance of a selected list of the organisms encountered in these studies is given in Table 6. In this table the figures are the percentage of total organisms.

Most of the net samples contained a considerable abundance of plankton, with the exception of the sample from one-half mile off Fort Myers beach which was relatively impoverished. However, detailed comparisons of plankton volumes are not feasible because the samples were taken for varying lengths of time, and in some of the yellow water areas the net quickly became clogged with a slimy material (see later discussion of the material) presumably associated with *Gymnodinium brevis.*

YELLOW WATER

The yellow or yellow-green discoloration of the water observed during the collecting period, and associated with dying fish, is apparently caused by an unarmored dinoflagellate, *Gymnodinium brevis* newly described elsewhere by Davis, (1947). This species contains several yellow-green chloroplasts, and occurred in countless millions. Analysis of the preserved sea water sample taken on January 18th in the worst water in Matanzas Pass shows 13,900,000 specimens per liter, yet, from field reports, much brighter yellow water was encountered one mile south of Useppa Island on January 28th. Undoubtedly the number of organisms per liter there would have been much higher. Microscopic examination of this water in the field showed that it consisted of overwhelming numbers of *Gymnodinium brevis* with large numbers of invertebrate larvae. Analysis of the preserved concentrated or net samples made several days later showed that other organisms were present. Dying

TABLE 6. Analyses of plankton organisms as explained in text numbers are percent of total organisms.

Sample	Selected Organisms															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Gymnodinium brevis	15.5	3.5	5.6	4.5	.....	.....	25.0	4.0	10.5	8.0	44.2	4.0	5.5	+	4.0	.....
Trichodesmium	1.0	.....	.....	.....	.....	.....	.....	.....	+	.....	10.7	9.0	3.7	.....	.....	.....
Chaetoceras spp.	18.5	10.0	35.6	38.5	0.5	0.5	6.0	6.5	9.0	13.5	10.9	25.5	.....	.....	26.0	27.0
Coscinodiscus (radiatus?)	+	4.0	2.0	.....	+	+	1.0	4.0	2.5	3.0	0.2	.....	.....	.....	+	+
Naviculoids	22.0	6.0	14.4	13.0	+	1.0	23.0	17.0	43.5	26.0	1.2	4.5	5.0	0.7	3.0	1.5
Nitzschia closterium	1.5	0.5	6.4	2.0	.....	0.5	37.0	39.5	12.0	20.5	0.4	2.5	0.3	78.5	2.0	4.5
Rhizosolenia (setigera?)	22.0	34.0	7.2	26.5	99.5	97.5	2.5	12.5	5.5	2.0	12.8	9.0	0.3	.....	17.0	33.5
Rhizosolenia robusta	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	38.4	18.2	.....	.....
Skeletonema Costatum	3.0	0.5	0.4	2.0	.....	.....	3.0	.....	2.0	4.5	9.6	32.0	.....	.....	24.0	17.5
Larval polychaete	+	.....	.....	+	+	+	+	+	.....	.....	0.2	+	.....	.....	.....	+
Polychaete postlarva	.....	.....	.....	.....	.....	.....	.....	.....	0.5	.....	1.0	.....	.....	.....	.....	.....
Gastropod veliger	+	6.5	0.8	.....	+	+	.....	1.0	1.0	.....	+	+	0.8	.....	.....	+
Lamellibranch larva	0.5	3.0	0.8	+	+	+	+	1.0	0.5	1.0	+	+	0.3	.....	.....	+
Copepodid stages (Calanoida)	0.5	10.0	0.4	+	+	+	+	4.0	1.0	+	+	+	0.8	+	+	+
Oithonina nana	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	17.0	1.2	+	+

fish were encountered three and one-half miles off Content Keys on April 18th when *Gymnodinium brevis* was present to the extent of only 420,000 cells per liter. See Table 7 for analyses of unconcentrated sea water samples.

TABLE 7. Cells per liter of *Gymnodinium* sp.

Location	*Date*	*Cells per liter*
Matanzas Pass	January 18	13,900,000
Gulf side, Captiva Island	January 24	2,640,000
Same Location	January 25	370,000
2 miles off Redfish Pass	January 25	93,200
5 miles off Captiva Island	January 25?	5,920
Pine Island Sound, off Captiva	January 25?	490,000
Off Content Keys	April 12	420,000
Off Barracuda Key	April 12	107,000
¼ mile S. of Redfish Pass	June 25	00,000

The brownish-yellow water taken in the Gulf off Redfish Pass on June 25 was not the same color as the saffron yellow water previously described as being caused by Gymnodinium; neither was it viscous. Analyses of both preserved and unpreserved samples of this water showed the only organism present in any great abundance was a tiny green flagellate, eleven microns in length, with four flagellae. There were 10,000,000 of these organisms per liter in preserved sea water. Species and genus remain undetermined, but it belongs to the family Cateriidae.

In the net samples from yellow water regions, the only cases where Gymnodinium did not amount to a large percentage of the total organisms were in the one from Clam Bay where a fish was seen dying and in the sample from off Content Keys. In the former sample Gymnodinium amounted to only 8.0% of the total organisms, being exceeded by tiny specimens of *Nitzschia closterium* and naviculoid diatoms, also small. The latter sample contained an even smaller percentage of Gymnodinium. In the yellowest water encountered, south of Useppa Island, Gymnodinium amounted to 44% of the total organisms. At this locality *Trichodesmium* sp., *Rhizosolenia (setigera?)* and *Skeletonema costatum* were also important ingredients of the smaller plankters.

The Useppa water was also characterized by enormous numbers of post-larval polychaetes. These entered into the plankton counts only to the extent of 1.0% of the total organisms, but because of their relatively large size it was clear that they constituted the bulk of the sample.

Gymnodinium brevis constituted 25.0% of the total organisms at the mouth of Blind Pass on January 21, in another patch of yellowish water. Here, as in Clam Bay, large numbers of *Nitzschia closterium* and naviculoids also were found, whereas these types were nearly absent from the Useppa Island samples. Water samples taken at Sarasota during the outbreak of July 18 contained over 60,000,000 cells of Gymnodinium per liter.

WATERS CLOSE TO YELLOW WATER AREAS

Net samples in areas near yellow water, but themselves in water of more normal appearance, were taken at two stations in Roosevelt Pass on January 21st, at the station at the mouth of Boca Grande Pass on January 28th and at the station off Barracuda Key on April 12th. These showed nominal numbers of Gymnodinium. At the dock in Roosevelt Pass they constituted 4.0% of the total organisms, at the upper end of Roosevelt Pass 10.5%, at Boca Grande Pass 4.0% and off Barracuda Key less than 1.0%. In Roosevelt Pass, *Nitzschia closterium* and naviculoids were the most numerous organisms present, while at Boca Grande Pass *Skeletonema costatum* and species of Chaetoceras were most abundant. Off Barracuda Key, *Nitzschia closterium* and *Rhizosolenia robusta* were far more numerous than any other forms in the net sample.

The sample from off Bonita beach on June 25 is comparable to that just described. Gymnodinium constituted 4.0% of the total organisms in the sample, while *Skeletonema costatum*, species of Chaetoceras, *Rhizosolenia* (*setigera?*) and Bacteriastrum amounted to 24.0, 26.0, 17.0, and 15.0%, respectively of the total organisms.

A sample obtained in Estero Bay on the same day showed the same diatom species dominant. *Rhizosolenia* (*setigera?*) amounted to 33.5%, *Chaetoceras* spp. to 26%, *Skeletonema costatum* to 15% and *Bacteriastrum* sp. to 10.5%. No *Gymnodinium brevis* were encountered.

RED WATER

In the region of the Gulf side of Fort Myers beach the water was red or reddish-brown in color. The numbers of Gymnodinium present were small. Three hundred yards offshore they amounted to 3.5%, and one-half mile offshore they amounted to 5.6%. The net samples showed large numbers of Copepoda. Nearly all of these were male, female and juvenile *Acartia tonsa*, but a few specimens of *Labidocera aestiva* and occasional cyclopoids and harpacticoids were also found. In the sample from three hundred yards off Fort Myers beach, Acartia constituted an extremely large proportion of the total plankton, considering that it is relatively large compared to the other abundant forms present. *Acartia tonsa* males constituted 2.0% of the total organisms, females constituted 6.5%, and juveniles constituted 2.0%. Thus, there was a total of 10.5% *A. tonsa* in the sample. In addition, Acartia nauplii were present in considerable numbers. Gastropod veligers and lamellibranch larvae were unusually numerous at the station three hundred yards offshore.

Animal plankton, chiefly copepods, predominated in the reddish water areas. The copepods did not cause the discoloration of the water, however, since they were more abundant at places where the water was only slightly turbid and not discolored. The red water areas followed the mass mortality of marine animals and was already found in areas where large amounts of fishes were floating and decaying in the water. Just off Fort Myers beach the copepods from a net sample, sample number two, Table 5, seemed to be mostly dead or moribund when examined immedi-

ately under the microscope. Possibly they were killed by the products of large amounts of organic decay. This condition led Mr. Thomas S. Austin, of the Hydrographic Office, Navy Department, to suggest that the reddish discoloration could have been caused by the presence of large numbers of purple sulphur bacteria. No examinations for bacteria were made.

WATER REVERTED TO NORMAL

At the Gordon Pass station the most abundant organisms were species of Chaetoceros amounting to 38.5% of the total organisms, and *Rhizosolenia* (*setigera?*), amounting to 26.5%. Animal types were present, but not abundant. Of the larger species, such as the Copepoda, very few were in the sample. Several specimens of *Labidocera aestiva*, of a second undetermined species of Labidocera, and of *Acartia tonsa* were observed.

The samples from off Naples, in the Gulf, consisted almost entirely of Copepoda (these formed the vast bulk of the sample) and of the diatom, *Rhizosolenia* (*setigera?*). The latter, being much smaller in size than the copepods amounted to 99.5% and 97.5% of the total organisms in the samples taken respectively one mile and three miles off Naples.

Analyses of the larger Copepoda found in these tows, and also in the April tows in the Key West area, are shown in Table 8.

TABLE 8. Larger Copepoda found at four selected stations.
The figures are percentage of total copepods.

Species	Sample No. 5	Sample No. 6	Sample No. 13[1]	Sample No. 14[1]
Acartia tonsa	3	1	1	–
Acartia tonsa	4	–	–	–
Acartia juv.	1	–	–	–
Centropages furcatus	10	12	10	25
Centropages furcatus	17	26	11	15
Centropages juv.	21	46	23	9
Eucalanus subcrassus	–	–	2	9
Eucalanus subcrassus	–	–	12	18
Eucalanus juv.	–	6	13	11
Labidocera aestiva	3	1	–	–
Labidocera aestiva	9	–	–	–
Labidocera juv.	30	3	1	–
Paracalanus parvus	–	–	6	2
Paracalanus parvus	1	4	6	6
Paracalanus juv.	–	–	16	2
Other Calanoida	–	–	–	3
Cyclopoid juv.	1	–	–	–
Harpacticoid	–	–	1	–

[1]In these samples the dominant copepod as far as numbers are concerned, was *Oithonina nana*. It, however, was omitted from the table because of its small size.

WATERS NEAR KEY WEST

Upon investigation of the Gulf waters off Key West after the April report of fish mortality in that region, many dead fish were discovered, and some in the process of dying were found three and one-half miles off Content Keys. The water there was of a greenish color, and the plankton was extremely abundant. Living specimens of *Gymnodinium brevis* were found, and numerous copepods were present, which together may account for the color of the water. Gymnodinium appeared to have a tendency to float near the surface, where they were numerous (420,000 cells per liter). They amounted to only 5.5% of the total organisms in the net plankton sample, which was taken about seven to ten feet below the surface.

The large diatom, *Rhizosolenia robusta*, was extremely abundant, amounting to 38.4% of the total organisms, while *Nitzschia longissima* accounted for another 15.4% of the total organisms in the net plankton. Copepoda were unusually abundant. The most numerous was *Oithonina nana*, the immature and mature stages of which amounted to 17.% of the total organisms. However, Oithonina was exceeded in bulk by *Centropages furcatus* and probably also by the pelagic decapod, *Lucifer* sp. In addition, Echinospira larvae and larval Brachiopoda were unusually abundant, while common copepods in addition to those already mentioned, were *Eucalanus subcrassus* and *Paracalanus parvus*.

A second station was established off Barracuda Key, where no dead or dying fish were observed, and where the water was much more nearly its normal color. Here *Gymnodinium brevis* occurred to the extent of 107,000 cells per liter at the surface, and amounted to less than 0.2% of the total organisms in the net sample, which again was taken at a depth of seven to ten feet. The smaller species of plankters were much less abundant in general than off Content Keys. The most numerous organism was the tiny diatom, *Nitzschia closterium*, which amounted to 78.5% of the total organisms. In actual numbers, per liter, *N. closterium* was about 175 times as abundant there as off Content Keys. Second most abundant in numbers was the much larger *Rhizosolenia robusta*, but its actual numbers per liter were only about one-third what they were at the Content Keys station. It amounted to 18.2% of the total organisms. Most other small types occurred in much smaller numbers per liter off Barracuda Key than off Content Keys.

Of the larger types, the adults of the various common copepods, except Oithonina, occurred in essentially the same numbers per liter at both stations, but the immature (copepodid) stages were much less numerous. This indicates a lessened breeding activity, associated with the decrease in the smaller plankton types.

SEQUENCE OF PLANKTON GROWTH

There was first the appearance of numbers of *Gymnodinium brevis* mixed in with other normal plankton types, mostly diatoms (as at the Boca Grande station). Locally, or over large areas there then appeared a "bloom" of Gymnodinium, and in these areas the mortality occurred. This was then followed by the decomposition of many dead organisms, with the consequent release into the water of much nutrient material. Bacteria and/or phytoplankton utilized this nutrient material, and then were themselves utilized, especially by the Copepoda, which consequently increased enormously in the plankton (as

at the Fort Myers stations). The Copepoda devoured all the suitable diatoms, and left only the species of Rhizosolenia, which would be very difficult for the copepods to handle (as at the Naples stations).

PRESENCE OF VISCOUS WATER ASSOCIATED WITH GYMNODINIUM

At the field station south of Useppa Island, it was observed that the yellow sea water was viscous. Upon taking up the water in the hands, it would string out instead of pour. Gilbert M. Smith (1938) reports the presence of pectic substances in a sheath in some dinoflagellates, but this he says to be rare. Kofoid & Swezy (1921) report numerous examples of unarmored dinoflagellates with a cyst wall, which is produced during the period of binary or multiple fission. However, the authors do not discuss the composition of this cyst.

It was considered possible that the viscous consistency of the water was caused either by many of these cyst walls that had been ruptured or by some substance secreted by the cells into the water. Another hypothesis was that this consistency was caused as a result of the decomposition of the many dead organisms.

The water decanted from the preserved sea water sample from Matanzas Pass, in the worst water locally available at that time, was very viscous, with physical characteristics between that of water and glycerol. Several chemical tests for protein and carbohydrate were made on samples of this water. All were negative except the Molisch test for carbohydrate, which was questionably positive.

Very small amounts of certain mucins and pectic substances will cause a great increase in the viscosity of water. It would seem that the substance causing the effect in the yellow water was not a protein, and therefore not due to the disintegration of dead organisms. Its possible nature, judging by the Molisch test, is some sort of carbohydrate—probably a pectinoid or a mucin.

CHEMICAL CHARACTERISTICS OF THE WATER

Surface samples were taken with a wooden bucket carefully to avoid introducing air bubbles. The temperature was determined immediately with a precision thermometer graduated to 0.1° C. The sample for the determination of dissolved oxygen was drawn off through a siphon tube from the bottom of the bucket.

Bottom samples were collected through a long hose attached to a small bilge pump. Many small air bubbles were introduced into the samples by this apparatus; therefore dissolved oxygen determinations on these bottom samples are considered erroneous and should be ignored.

Because no adequate pH apparatus was available, only approximate pH determinations were possible, using phenol red in test tubes, and matching the colors with the printed color chart of Clark (1928).

Analytical methods used were those described in mimeographed "Methods of Oceanographic Chemistry," prepared by Rex J. Robinson and Thomas G. Thompson, Oceanographic Laboratories, University of Washington. Chlorinity determinations were made using a modification of the Mohr method. Dissolved oxygen was determined by the Winkler method. Phosphate-phosphorus was determined by the modified Deniges method. Nitrite-nitrogen was determined

TABLE 9. Results of analyses of sea water.

Sample No.	Location	Depth ft.	Date 1947	Temp. °C.	pH	Sal. o/oo	Chl. o/oo	Oxygen ml/L	Oxygen % sat.	H_2S	PO_4	NO_2
A	300 yds. SW Ft. Myers Beach	0	1-18	24.9	8.2	37.0	20.5	5.24	108.8	....	....	....
B	2 mi. SW Ft. Myers Beach	0	1-18	24.8	8.2	36.4	20.1	5.28	108.3	....	....	....
C	2 mi. SW Ft. Myers Beach	18	1-18	25.0	8.2	36.2	20.0	5.06	103.8	....	....	....
D	N bridge, Matanzas Pass	0	1-18	25.8	8.2	36.7	20.3	3.29	69.0	....	....	....
E	Dock, E side Matanzas Pass	0	1-18	26.1	8.2	36.9	20.4	3.25	68.6	....	....	....
F	Dock, E side Matanzas Pass	12	1-18	25.6	8.2	37.0	20.6	6.78	142.4*	....	....	....
G	12 mi. SSW Ft. Myers Beach	0	1-18	23.9	8.2	37.0	20.6	4.84	98.6	....	....	....
H	12 mi. SSW Ft. Myers Beach	40	1-18	23.6	8.2	36.6	20.2	....	....	....	....	....
I	Buoy, 2.5 mi. S, Myers Beach	0	1-18	24.8	8.2	36.6	20.2	4.61	94.8	....	....	....
J	Buoy, 2.5 mi. S, Myers Beach	17	1-18	....	8.2	36.6	20.2	....	....	....	....	....
K	3 mi. W of Gordon Pass near Naples	0	1-19	24.5	8.2	36.4	20.1	4.23	86.3	....	....	....
L	3 mi. W of Gordon Pass near Naples	22	1-19	....	8.2	36.4	20.1	....	....	....	....	....
M	1 mi. W of Gordon Pass	0	1-19	24.4	8.2	36.7	20.3	4.74	97.0	....	....	....
N	1 mi. W of Gordon Pass	19	1-19	....	8.2	36.6	20.2	....	....	....	....	....
O	Near dock in Gordon Pass	0	1-19	25.2	8.2	36.6	20.2	5.15	106.6	....	....	....
P	1 mi. SE of Useppa I.	0	1-28	24.1	...	36.6	20.2	1.58	32.2	....	....	....
Q	2½ mi. N of Content Keys	0	4-12	26.4	8.3	35.5	19.7	5.36	111.6	....	0.00	0.00
R	2 mi. N of Barracuda Keys	0	4-12	27.0	8.3	35.8	19.8	5.50	116.5	....	0.00	0.00
S	½ mi. off Big Hickory Pass, Bonita Beach	0	6-25	....	...	30.6	16.9	....	....	....	....	....
T	Estero Bay	0	6-25	....	...	21.4	11.9	....	....	....	....	....
U	Off Bonita Beach	0	6-25	....	...	33.5	18.6	....	....	....	....	....
V	"Yellow water" off Redfish Pass, Captiva I.	0	6-25	....	...	33.1	18.3	....	....	....	....	....

*Inaccurate because of air bubbles from sampling apparatus.

by the modified Griess method. Complete references for these methods are cited in Williams (in press).

Rough qualitative tests for hydrogen sulfide were made with lead acetate paper. No clearly positive tests were obtained.

Results of all analyses are summarized in Table 9.

Comparing these results with those of normal sea water at various stations in south Florida (Williams in press), one may conclude that the temperatures, pH values, and salinities are not abnormal. Only three of the oxygen values, samples D, E, and P, would be considered abnormally low. The lowest value, 32.2% saturation, was found in the "saffron yellow," viscid water near Useppa Island. This water had 44.2% Gymnodinium, and more blue-green algae (Trichodesmium) than any other plankton sample, together with considerable numbers of diatoms. The other low oxygen values were found in Matanzas Pass where the water was discolored and contained 15.5% Gymnodinium and about 65% diatoms. The fact that fish were found dying at location of sample Q with 111.6% oxygen suggests that low oxygen was probably not the immediate cause of death.

The absence of phosphate in surface, inshore waters in south Florida is not unusual. Rather, it is to be expected where a large phytoplankton population has developed and utilized the available phosphate and nitrate. The absence of nitrite in April is somewhat unusual, but it might be explained by assuming rapid bacterial oxidation of the nitrite to nitrate and immediate utilization by the phytoplankton.

DISCUSSION

CAUSES OF THE MORTALITY

Associated with the two worst cases of yellow water encountered namely that in Matanzas Pass and south of Useppa Island, the water was characterized by low oxygen content, as indicated by analyses reported in Table 9. In Matanzas Pass the oxygen amounted to 3.25 ml. per liter, and at the Useppa Island station it amounted to only 1.56 ml. per liter. An oxygen content of 2.1 ml. per liter has been shown, by Ellis (1937) to be the lower limit for the normal respiration of fresh water fishes. Conditions are similar for most salt water types. Thus the oxygen tension at the Useppa Island station would have been dangerous, or even lethal, to fishes and other organisms.

Gymnodinium brevis which was so abundant at the two stations with low oxygen content, could not have been the direct cause of the low oxygen tension, inasmuch as these are holophytic organisms (none of those examined showed any signs of ingested food, and yellow-green chromatophores were present). Gymnodinium species, however, are very delicate organisms and many may have perished in the crowded conditions of the yellow water, and those undergoing disintegration may have used up the oxygen. Also, at the Useppa Island station, there were large numbers of post larval Polychaeta, constituting the bulk of the plankton in the net samples, and these may have used up the oxygen. There was no evidence of a similar condition in the worst water of Matanzas Pass, but here no net sample was taken, though one was obtained nearby.

The authors did not see any mass mortality of fishes as recounted by Mr. Darling, but they were commonly reported. A few fishes were seen dying, one in the bright yellow water in Pine Island Sound and another in water behind Captiva Island, which was yellowish-green in color. In slightly turbid water from Florida Bay north of Content Key, four or five fishes were seen dying and some of them were captured with a dipnet. They showed the general reactions of fishes which are poisoned or being asphyxiated. The stomachs contained no food and the gills were not occluded by mucus. There were no signs of lesions or abnormalities which could be detected by gross examination. The oxygen content of the water was 5.34 ml. per liter (111.6% saturated) at that locality.

Fishes were found dying in discolored water which showed normal temperature, pH, salinity, dissolved oxygen, and mineral content. At the same time, fishes were found alive and apparently healthy in normally colored water with similar physical and chemical properties. This suggests that the immediate cause of death is probably to be found in the plankton conditions.

A carboy of the Florida Bay water was brought back to the laboratory at the University of Miami. The dinoflagellate, *Gymnodinium brevis,* was found alive in the water at the laboratory. Twelve fishes from Biscayne Bay all died in four and one-half days when placed in the water. An equal number of controls in Biscayne Bay water all lived. Both samples of water were placed in glass aquaria side by side and both were strongly aerated by means of electric pumps. In the Florida Bay water eight *Cyprinodon variegatus* died in twenty to forty-six hours. Two puffers, *Spheroides testudineus,* died in forty-eight hours. Two mojarras, *Eucinostomus gula,* died in eighty-eight to one hundred and eighteen hours. Two crabs, *Portunus sayi,* did not die in the water in a week and it was assumed they were relatively or completely immune. All fishes and crabs in the control aquarium, that contained the same numbers of species of comparable sizes, lived, except one puffer which hopped out on the floor during the third night and was found dead next morning.

One week after the last fishes had died in the aquarium of Florida Bay water, the control fishes were placed in it. They survived for three weeks and the experiment was discontinued. This indicates that the original "poison" had been absorbed or taken up by the fishes it killed, or the initial concentration and any which was subsequently produced had been broken down or undergone chemical change rendering it innocuous.

Samples of the brownish-yellow water taken on June 25, containing the unknown flagellate were brought back to the laboratory. A similar experiment to that described was set up and *Cyprinodon*

variegatus were placed in both aquaria. Baby fish died quickly in each one. Eleven fish in the control aquarium had all died at the end of a week, while three out of eight originals survived in the discolored water. It was concluded that there was no indication of poisonous quality in the water that contained the unknown flagellate.

Obviously death was not caused by lack of oxygen either in Florida Bay or in the laboratory. The dinoflagellate, *Gymnodinium brevis,* was the only constant factor associated wtih all waters where fishes were dying. They were not present in vast numbers in Florida Bay and yet fishes died slowly in the laboratory when placed in the water. In patches of the yellow water, where *Gymnodinium brevis* was in great abundance, fishes were commonly reported to be quickly killed upon entering it. Such water was viscous so that fishes in it may have had mechanical difficulty in breathing, but nevertheless, such difficulties were not present in much of the water where fishes died. These observations in addition to the simple laboratory experiments indicate that there is some substance given off by or associated with *Gymnodinium brevis,* possibly released from its broken down cells, which is poisonous to marine animals.

One commonly reported observation in the field suggests that fishes may be injured by or killed very slowly by the poison in sea water. It was reported at several times from different places, one account coming from experience with the 1916 mortality, that schools of mullet surrounded by net fishermen suddenly died when they became excited or disturbed and swam wildly about. Such similar accounts from different times and places strengthen the suggestion that the fishes may have been suffering from some respiratory disturbance which did not become fatal until they were disturbed and their activity was increased under excitement. Coates (1933, p. 26) describes an instance where a marine fish was placed in fresh water where it lived well so long as it was undisturbed, "but at the slightest nervous shock, such as the clapping of hands three feet away, it turned on its back and died—immediately."

During a case of similar mortality on the Texas coast a peculiar, strong but odorless gas, causing burning of the eyes and respiratory passages was reported by Lund (1936). A similar gas was given off by the sea water around Captiva Island and was especially noticeable when a heavy surf was rolling in. Inhabitants of some parts of the island coughed incessantly and some of them had difficulty in sleeping. The authors encountered the gas several times around Captiva Island and found that it was released when the sea water was boiled or heated. By the same method it was found to be present, although only faintly perceptible from the waters of Florida Bay north of the Keys. This gas was present at Captiva far into February, long after mortality of fishes had ceased, and after some lives fishes had returned to the area, as shown by catches of sports fishermen. Thus it is apparent that this substance was not the cause of mortality. It was not hydrogen sulphide, or sulphur dioxide, which would not be expected in sea water, as shown by chemical tests as well as the lack of odor. Lund (1936) has suggested that this substance is probably a product of the decay of organic materials in sea water. In all probability this opinion is correct but the identity of the substance remains unknown.

The presence of hydrogen sulphide, at least during the early part of the outbreak is indicated by blackened boats at Naples. These boats were painted with white lead and had traveled through the areas of "bad" water. Hydrogen sulphide is often produced when there is heavy mortality of marine animals at sea, as had been described in several cases, especially with respect to El Nino of the Peruvian coast and Walfisch Bay in South Africa. Upon the death and decay of large masses of protoplasm oxygen is used up and decay proceeds under anaerobic conditions with the production of hydrogen sulphide. Although, hydrogen sulphide is a poison which could aggravate the situation and probably does, it is generally conceded (Brongersma-Sanders 1943), that hydrogen sulphide is a result rather than an initiator of the mortality. The small localized instances, such as that described by Gunter (1942), where hydrogen sulphide is thought to be the cause of mortality, are special cases.

The presence of hydrogen sulphide may account for the dead turtles and porpoises seen by the mackerel fisherman. On the other hand these air breathers may have succumbed from eating the poisoned fishes. The notorious California mussel poison, which is occasionally fatal to human beings, is known to come from a dinoflagellate, Gonyaulax, which sometimes blooms in great abundance in California waters (Sommer, Whedon, Kofoid, & Stohler 1937).

Conditions Leading to the Plankton Bloom

The limiting factors of phytoplankton growth are nearly always, according to Liebig's law of the minimum, the presence of the nutrient salts nitrates, nitrites and phosphates. It is well recognized that these salts are commonly less abundant in warm or tropical waters than in temperate and cool waters. It is also known that the dinoflagellates can grow or flower at lesser minimum concentrations of these materials than can the diatoms. Dinoflagellates also seem to prefer warmer waters and therefore blooms or discolorations of the water produced by them occur more commonly in southern waters than they do in colder zones.

In most cases of mass mortality of marine animals caused by plankton blooms, one or other species of dinoflagellate has been more or less strongly indicated as the causative agent. For example, Sommer, Whedon, Kofoid, & Stohler (1937), *vide supra,* have shown that Gonyaulax is poisonous.

Reports show a definite recurrence of fish mass mortality on the lower coast of West Florida every twelve years or so on the average, but at very irregular intervals. Because the phenomenon, as reported

by residents of that coast and in the literature, has been similar each time, there is a strong presumption that past outbreaks had the same cause as the 1946-47 outbreak, namely a vast flowering of dinoflagellates. Water discolorations without mortality have not been reported from the region, though they may nevertheless have occurred. The scattered and incomplete reports of previous occurrences indicate that they are not associated with particular seasons of the year, and the present disturbance has covered all but the fall months.

Plantkon blooms are often associated with weather disturbances or weather alterations which may bring about change in water masses or upwellings. This is true in South Africa (Gilchrist 1914), India (Hornell 1917), California (Sverdrup, Johnson & Fleming 1946), and in the abnormal progress of the Equatorial Counter-current southward (Schott 1931). El Nino is accompanied by excessive rains abnormal to the Peruvian coast (Murphy 1926), and the cases of fish mortality in Texas (Lund 1936, Burr 1945), were likewise preceded by excessive rains. Furthermore, excessive rains preceded the 1916 episode of fish-mortality in Florida. Heavy rains preceded the second outbreak of mortality in the Fort Myers area in June, 1947. The average monthly rainfall for June for the Fort Myers area for the previous 53 years has been 8.91 inches. For the first 25 days of June, 1947 the rainfall was 10.30 inches and 9.42 inches of this fell between June 8 to 18, inclusive. The brown water that drained from the mangrove swamps and bays out into the Gulf led some local residents to believe that "tannic acid" was killing the fish.

The weather data taken at the Fort Myers Weather Bureau station during October, November, December, 1946 and the first half of January, 1947 are given in Table 10. These data show that the monthly temperatures were higher than average when compared with the previous fifty-three years, and that the rainfall was less. The direction of the prevailing winds was not greatly different from other years. It was reported generally that during the fall months it was unusually hot and still, and several people attributed the fish-mortality to the "hot weather." Additional abnormal weather in this area was a hurricane which came ashore on the west coast of Florida on October 7, 1946. The wind blew offshore at eighty miles an hour at Fort Myers. Possibly the sequence of high offshore winds in October and hot still weather in November produced conditions favorable for the bloom.

Little is known of the details of the water currents of the Gulf of Mexico, but it is generally agreed, as stated by Sverdrup, Johnson, & Fleming (1946, p. 641): "In the Gulf of Mexico several large eddies exist, and all of these appear to be semipermanent features, the locations of which are determined by the contours of the coast and the configuration of the bottom." The ordinary inshore current of the West Florida coast seems to be north and it seems to be part of a large eddy of the eastern Gulf. Meteorological conditions might well bring about

TABLE 10. A summary of the weather data gathered at the Fort Myers, Florida, Weather Bureau station, October, 1946-January, 1947.

Temperature averages compared to the previous fifty-three years.

	October		November		December		January	
	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum	Min. First half only
1946-47	87.6	67.8	80.5	65.5	79.6	58.1	83.4	62.6
1892-44 53 years	83.8	68.0	75.9	60.5	74.2	55.6	73.4	54.2

	Rainfall			
	October	November	December	January ½ only
1946-47	1.34	3.39	0.57	0.48
Ave. 1892-44	4.48	1.33	1.56	0.88

	Prevailing Wind			
	October	November	December	January
1946-47	N.E.	N.E.	N.E.	N.E.
1892-44	N.E.	N.	N.E.	N.W.

changes in these eddies or currents, which possibly would allow an upwelling, and it is well known that upwellings are important in bringing nutrient salts up to the euphotic zone.

There is no definite knowledge that an upwelling did occur. However, throughout the world the most noticeable upwellings occur on western coasts rather than eastern coasts, and in Florida the recurrence of mortality has been on the west coast, and not on the east coast. It is true that the peninsula of Florida is extended as a wide, shallow underwater shelf on the west coast. The edge of the continental shelf is approximately 150 miles offshore. This configuration of the bottom would seem to be unfavorable for the occurrence of major upwellings. However, studies cited by Sverdrup, Johnson, & Fleming (1946, p. 501) have shown that water is drawn to the surface from depths not exceeding two hundred to three hundred meters and in some cases the upwelling may be from depths as shallow as forty meters. Pierce (1883, 1884) maintained that fishes off the west coast of Florida were killed during 1880 by cold water originating from the depths. He stated that this mortality was preceded by offshore hurricane winds which caused an overtow and rising of cold water and added that dead fish on the west coast of Florida always follow hurricanes blowing from land or from the southwest. It seems probable, however, that upwellings from such shallow depths, unless very violent, would not bring about an increase of nutrient salts, inasmuch as forty meters is well within the euphotic zone.

Another hypothesis considered to have possible bearing on the changes of water masses on the lower

West Florida coast concerns seismic disturbances. Earthquakes occurred in Santo Domingo from August 4 to 8, 1946. Changes of about a foot in the water level depths of twenty water wells in the Miami region took place suddenly coincident with these quakes, according to records kept by the U. S. Geological Survey. Taylor (1917) raised the question of seismic disturbances in his report on the fish mortality of 1916 on the West Coast of Florida. There are to our knowledge no observations showing that seismic disturbances cause upwellings, but the matter is one to be considered as a possible factor in the situation

On the other hand, in the absence of any data concerning the plankton or the hydrography of the region previous to the dinoflagellate bloom, we must also consider the possibility that no change in the total phosphorus and nitrogen occurred. This would obviate the necessity of postulating an upwelling. If there were no change in the nutrient salt content of the water, such factors as a change in light intensity, a raised water temperature, selective feeding by zooplanktonts, retardation of the growth of other phytoplanktonts due to the presence of numbers of *Gymnodinium brevis*, the self stimulation of *G. brevis* by the action of by-products of its own growth activities, or a combination of two or more of these factors could have given *G. brevis* the advantage over other phytoplanktonts originally present in the plankton. A source of increased phosphate in the coastal waters may be the rivers which pass through the phosphate bearing areas of inland Florida. The very wide extent of the outbreak would seem, however, to preclude this possibility. It is also reasonable to consider the likelihood of submarine outcrops of phosphate rock over a wide area. This would scarcely explain the long quiescent periods between outbreaks of mortality, however.

Another possibility which may not at present be examined in detail owing to the absence of data is that the nutrients necessary for a great increase in the total amount of plankton may normally be bound up as dissolved organic material or bacteria or in some other phase of the nutrient cycle but that a change in physical conditions might release them in a form available to the plankton. It may even be possible that large amounts of nutrient are normally present in the bottom muds in colloidal or adsorbed form and that they are periodically released following abnormal weather conditions. It is proposed in the future to investigate fully the factors entering into the frequently observed sudden blooms of only one species of phytoplankton, or one group of closely related types when the obvious environmental factors such as temperature, nutrients, etc., would seem to be favorable to all phytoplankters. The fundamental relationship between dissolved mineral nutrient and other phases of the nutrient cycle, including bacteria and bottom muds also require careful study. Tropical waters have been largely neglected in this respect.

SUMMARY

1. A mortality of marine fishes and other animals of catastrophic proportions took place along the lower West Florida coast between November, 1946 and August, 1947.

2. In isolated places, and not in regular association with dying fish, low oxygen tension was found. This may have been associated with the decay of large numbers of dead animals and is to be considered a result rather than a cause of the mortality. The chemistry of the sea water was not found to be abnormal.

3. The mass death of marine organisms was associated with the flowering of dinoflagellate, *Gymnodinium brevis*. Water that contained this organism killed fishes in an aerated aquarium and fishes were found dying in its presence in the sea, although the oxygen content was high. In some places *Gymnodinium brevis* reproduced so abundantly that patches of the water became saffron yellow in color and noticeably viscous. Schools of fishes entering this water died immediately. It is concluded that *Gymnodinium brevis* like certain related dinoflagellates, is specifically poisonous to marine animals when present in large numbers.

4. The weather was abnormally warm and still and a hurricane wind blew offshore on the lower Florida Gulf Coast during the fall of 1946. It is suggested that changed meteorological conditions or other factors may have brought about changes of the water masses which increased the supplies of nutrient salts and led to a flowering of the plankton, especially *Gymnodinium brevis*. The more remote possibility of seismic disturbances is also considered together with the possibility of causative factors other than an increase of nutrient salts.

5. Records of similar catastrophic mortalities localized along the lower West Florida Coast go back to 1844, and it is suggested that these instances had similar causes.

6. Fishes found dead along the beaches show that the families of fishes of greatest abundance in lower Florida are quite different from those of the northern Gulf Coast and a transition from a temperate to a tropical fauna is indicated.

LITERATURE CITED

Brongersma-Sanders, M. 1943. De jaarlijksche Visschensterfte bij Walvisbaai (Zuidwest-Afrika) en haar Beteekenis voor de Palaeontologie. Overdruk uit Vakblad voor Biologen **24**(2): 13-18.

Burr, J. G. 1945. Science tackles a mystery. Texas Game and Fish **3**(9): 4-5, 24-25.

Coates, C. W. 1933. Tropical fishes for a private aquarium. Garden City, New York. XI + 226.

Clark, W. M. 1928. The determination of hydrogen ions. Baltimore. 3rd ed.

Davis, C. C. 1947. Gynodinium brevis n. sp., a cause of discolored water and animal mortality in the Gulf of Mexico. Bot. Gaz. **109**(3): 358-360.

Ellis, M. M. 1937. Detection and measurement of stream pollution. Bull. U. S. Bur. Fish. **48**: 365-437.

Gilchrist, J. D. F. 1914. An enquiry into the fluctuating fish supply on the South African Coast. Cape Good Hope Marine Biol. Lab. Rep. **2**: 8-35.

Gunter, G. 1942. Offatts Bayou, a locality with recurrent summer mortality of marine organisms. American Midl. Natulist. **28**(3): 631-633.

1945. Studies on marine fishes of Texas. Pub. Inst. Marine Sci. **1**(1): 1-190.

Gunter, G., F. G. W. Smith, & R. H. Williams. 1947. Mass mortality of marine animals on the lower west coast of Florida, November, 1946-January, 1947. Science **105**: 256-257.

Hornell, J. 1947. A new protozoan cause of widespread mortality among marine fishes. Madras Fish. Bull. **11**: 53-66.

Kofoid, C. A. 1911. Dinoflagellates of the San Diego region. IV the genus Gonyaulax. Univ. Cal. Pub. Zool. **8**: 187-286.

Kofoid, C. A., & O. Swezy. 1921. The free-living unarmored Dinoflagellata. Mem. Univ. Calif. **5**: 1-538.

Lund, E. J. 1936. Some facts relating to the occurrences of dead and dying fish on the Texas Coast during June, July and August, 1935. In Ann. Rep. Game, Fish and Oyster Comm. (1934-35) 47-50.

McKernan, D. L., & V. B. Scheffer. 1942. Unusual numbers of dead birds on the Washington Coast. The Condor **44**: 264-266.

Murphy, R. C. 1926. Oceanic and climatic phenomena along the west coast of South America during 1925. Geogr. Rev. **16**: 26-54.

Nishikawa, T. 1901. Gonyaulax and the discolored water in the Bay of Agu. Hunot. Zoological Japonensis.

Otterstrom, C. V., & E. Steeman. 1940. Two cases of extensive mortality in fishes caused by the flagellate, Prymnesium parvum Carter. Rept. Danish Biol. Sta. **44**.

Pierce, H. D. 1883. An opinion of the cause of mortality of fishes in the Gulf of Mexico. Bul. U. S. Comm. Fish and Fisheries **3**: 332.

1884. Notes on the bluefish, mortality of Florida fishes, etc., ibid **4**: 263-266.

Schott, Gerhard. 1931. Der Peru-strom und seine nordlichen nachbargebiete in normaler und anormaler ausbildung. Hun. Hydrogr. **59**: 161-169, 200-213, 240-253.

Smith, G. M. 1938. Cryptogamic Botany. New York. 2 vols. viii + 545, vii + 380.

Sommer, H., & F. N. Clark. 1946. Effect of red water on marine life in Santa Monica Bay, California. California Fish and Game **22**: 100-101.

Sommer, H., H. W. Whedon, D. A. Kofoid, & R. Stohler. 1937. Relation of paralytic shellfish poison to certain plankton organisms of the genus Gonyaulax Arch. Pathology **24**: 537-559.

Sverdrup, H. U., M. W. Johnson, & R. H. Fleming. 1946. The oceans, their physics, chemistry and general biology. New York x + 1087.

Taylor, H. F. 1917. A mortality of fishes on the west coast of Florida. Science 367-368.

1917a. Mortality of fishes on the West Coast of Florida. Bur. Fisheries Doc. **848**: 1-24.

Torrey, H. B. 1902. An unusual occurrence of dinoflagellata on the California coast. Am. Nat. **36**: 187-192.

Whitelegge, T. 1891. On the recent discoloration of the waters of Port Jackson. Rec. Australian Mus. **1**: 179-192.

Williams, Robert H. 1947. Seasonal variations in ecological conditions in tropical inshore waters. In press.

THE VEGETATION OF THE WESTERN CROSS TIMBERS

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THE VEGETATION OF THE WESTERN CROSS TIMBERS

INTRODUCTION

More than a century ago, Kennedy (1841) of the British diplomatic corps introduced the Cross Timbers to literary persons, both here and abroad. He wrote: "The Cross Timbers of Northern Texas, which may be deemed one of the natural curiosities of the country, forms a remarkable feature in its topography. The following description of it is founded upon information furnished by respectable persons who have resided for several years in its vicinity, have visited nearly all portions of the adjoining districts, and examined it throughout its whole extent.

"The Cross Timber is a continuous series of forests, extending from the woody region at the sources of the Trinity, in a direct line north, across the apparently interminable prairies of northern Texas and the Ozark territory, to the southern bank of the Arkansas River. This belt of timber varies in width from five to fifty miles. . . . When viewed from the adjoining prairies on the east or west, it appears in the distance as an immense wall of woods stretching from south to north in a straight line, the extremities of which are lost in the horizon. . . . The trees composing these forests are not distinguishable by any peculiarity from those which are occasionally found in the adjoining prairies, or in the bottoms bordering the streams which intersect the Cross Timber. Oak, hickory, elm, white oak, post oak, holly and other trees are found in it. . . . The black jack, a species of oak, is met with throughout its whole extent, from the Arkansas to the 'Black Jack Ridges,' at the sources of the Trinity.

". . . As might naturally be supposed, the Cross Timber forms the great landmark of the western prairies; and the Indians and hunters, when describing their routes across the country, in their various expeditions, refer to the Cross Timber, as the navigators of Europe refer to the meridian of Greenwich. If they wish to furnish a sketch of the route taken in any expedition, they first draw a line representing the Cross Timber, and another representing the route taken, intersecting the former. Thus a simple, but correct, map of the portion of country traversed in the expedition is at once presented to view.

"The remarkable uniformity which characterizes the Cross Timber, and its apparently artificial arrangement, under a particular meridian, has induced some persons to believe that it is a work of art, and owes its origin to the unknown race of men who have erected the mounds and ancient fortifications of the Mississippi Valley. It is difficult to conceive, however, for what useful purpose it could have been intended, unless as a landmark to distinguish the boundary between two nations. But whether it be the work of art or of nature, will probably never be determined. The lines of civilization are rapidly extending towards it, and soon the scrutiny of science will be forever checked by the destroying axe of the pioneer."

Kennedy did not differentiate between the Eastern Cross Timbers and the Western Cross Timbers of Texas. They lie east and west of the Fort Worth Prairie, respectively. Actually, the Cross Timbers did not yield as readily to the axe as was anticipated. Also, had Kennedy himself visited the Cross Timbers he might have perceived that it occupied sandy soils, contrasting sharply with the clays of the adjoining prairies.

The origin of the name "Cross Timbers" is evidently not recorded but presumably alludes either to the fact that this forest extends north and south across, rather than along, the major streams all of which flow eastward; or to the fact that early westward travelers who had left the main body of the great eastern forest and entered upon open prairie found it necessary to cross yet another body of forest before entering upon the grasslands that extended to the Rocky Mountains.

The boundary of the area frequently called "Cross Timbers" in Oklahoma is very irregular and the main area is much interrupted by bodies of open grassland. This is the portion which Kennedy (1841) referred to as extending to the Arkansas River. Its location and extent have recently been mapped in detail as the Post oak-Blackjack oak type by Duck and Fletcher (1943).

At the north central boundary of Texas on the Red River the Cross Timbers divide into two discrete belts. These extend southward about 150 miles as continuous bodies of forest or savannah bounded by open prairie. The two belts, originally known as the Upper and Lower Cross Timbers, are now generally known as the Western and Eastern Cross Timbers, respectively. Both Upper and Lower Cross Timbers were commonly mentioned by Kennedy's (1841) contemporaries.

Quantitative data of the present study were all obtained in Texas upon the watershed of the Trinity River which is centrally located and is the major river basin of the Western Cross Timbers. Extensive travel and study of the Cross Timbers of both Oklahoma and Texas indicate that many of the findings in either state are applicable in both within the same rainfall belt.

Acknowledgments

The writer wishes to express appreciation to Mr. H. M. Bell, Range Conservationist, for numerous helpful suggestions during the progress of the study;

to Mr. S. E. Wolff, Agronomist, who aided in the identification of species; to Messrs, J. E. Engleman, W. E. Brandt, and D. L. Grissom, Range Conservationists, who helped with work on the cross-country transects; to Mr. E. W. Jenkins, Regional Photographer, for painstaking work in obtaining most of the photographs; to Mr. R. M. Marshall, Soil Scientist, for help in identification of soils and determination of acreages; to Mr. John O. Roy, Soil Scientist, who is largely responsible for the detailed boundary of the Western Cross Timbers and the delineation between Main Belt and Fringe based upon criteria established jointly; to Mr. L. P. Merrill, Regional Conservator, for use of his splendid library of early Texas literature; and to Dr. Lewis M. Turner, Forester, under whose direction field work was initiated. The men are all of the U. S. Soil Conservation Service except Dr. Turner, formerly Forester, U. S. Forest Service, now Dean of the School of Forest, Range, and Wildlife Management, Utah State Agricultural College.

Location and Area

The location and area of the Western Cross Timbers of Texas have been generalized on previously published maps. The most recent of these was provided by Carter (1931). An original detailed map of the Western Cross Timbers, showing both the main belt of sandy soils and the western fringe of rocky and gravelly soils, is shown in Figure 1.

The total area of the Western Cross Timbers as bounded in Figure 1 is 4,116,000 acres. Data of the Conservation Surveys Division of the U. S. Soil Conservation Service indicate an additional 150,000 acres of comparable soils in widely scattered outliers to the south and west. The area of the main belt is 2,436,000 acres. It is characterized by Red and Yellow Podzolic soils with gentle relief developed upon Cretaceous strata. The area of the Fringe is 1,680,000 acres. It is characterized by immature Reddish Prairie soils developed upon Pennsylvanian strata with rocks and gravel at the surface, and by greater relief. The sparse overstory of post oak *(Quercus stellata)* and blackjack oak *(Quercus marilandica)* characterizes both delineations though the understory vegetation differs greatly. Unshaded areas of the map both within and outside of these delineations have various other types of vegetation and soils apparently unsuited to survival of post oak and blackjack oak. The natural absence of these species was generally regarded as sufficient cause to exclude such areas from further consideration in the present research because the area of the "Cross Timbers" has been associated with the presence of these oaks since the earliest references. However, the vegetation of small "included prairies," with Reddish Prairie soils, is treated briefly under the description of the Prosopis type.

The Main Belt extends 150 miles south from the northern limit near the Red River (Texas-Oklahoma State line), curving westward at the southern extremity. The Main Belt and Fringe together, though much interrupted, occupy the major portion of an area 150 miles long, varying in width from about 25 miles at the north to about 110 miles at the south.

REVIEW OF ECOLOGICAL LITERATURE

No detailed account of Cross Timbers vegetation has previously been published. However, the area has received general treatment by several ecologists because of the apparent anomaly of the tree overstory within this portion of the great mid-continental grassland. Most early botanists evidently regarded the Cross Timbers simply as the western fringe of the great eastern hardwood forest, scrubby and savannah-like because of prairie fires or aridity or both.

Tharp (1926), who gave the first comprehensive account of Texas vegetation east of the 98th meridian, bounded and described the Cross Timbers. He regarded them as a part of the oak-hickory forest or Quercus-Carya Association of the deciduous forest formation. However, he recognized a *Quercus stellata* Consociation in the western and most xerophytic portion of the delineation. Tharp found that the rainfall over the Association in Texas varied from 45 inches at the east to hardly 30 inches at the west but that the soil was uniformly of sand underlaid by red or yellowish, or, sometimes, by grayish clay. He stated ". . . the well-known coarseness and porosity of such soils suggest corollary water relations as the controlling factor in its geographic distribution." Weaver and Clements (1938) interpreted the western portion of Tharp's delineation as follows: "Extensive areas of oaks, the Cross-Timbers, occur as two massive belts through central Texas and extend more or less broken into Oklahoma. These have usually been regarded as portions of the oak-hickory forest, but this is hardly true in the climax sense. They are composed almost wholly of post oak and blackjack, *Quercus stellata* and *Q. marilandica,* which are usually not true climax dominants. On careful examination, the Cross-Timbers have proved to be chiefly oak savanna, in which the grasses are climax dominants. The soil is typically light and sandy, and the oaks are relicts from a former moist phase of the climatic cycle that have been able to maintain themselves against the competition of the grasses by virtue of the favorable chresard of the sandy soil. In this prairie climate, the oaks constitute a postclimax, since the climax forest would return in the event of a shift to a wetter climate."

Bruner (1931) treated the ecology of the "Cross-Timbers" of Oklahoma under the heading "Oak-Hickory savannah." He, too, regarded it as an associes, pointing out "Climatically the area should be dominated by grasses but the open, porous soil permits the growth of trees and, in places, turns the balance decidedly in their favor." Bruner's description of general environment of the Quercus associes in Oklahoma is also largely applicable to the Cross Timbers of Texas. McBryde (1933), working to the east and south of the Cross Timbers, near the western edge of the Oak-Hickory Association as delineated by Weaver and Clements (1938), has shown con-

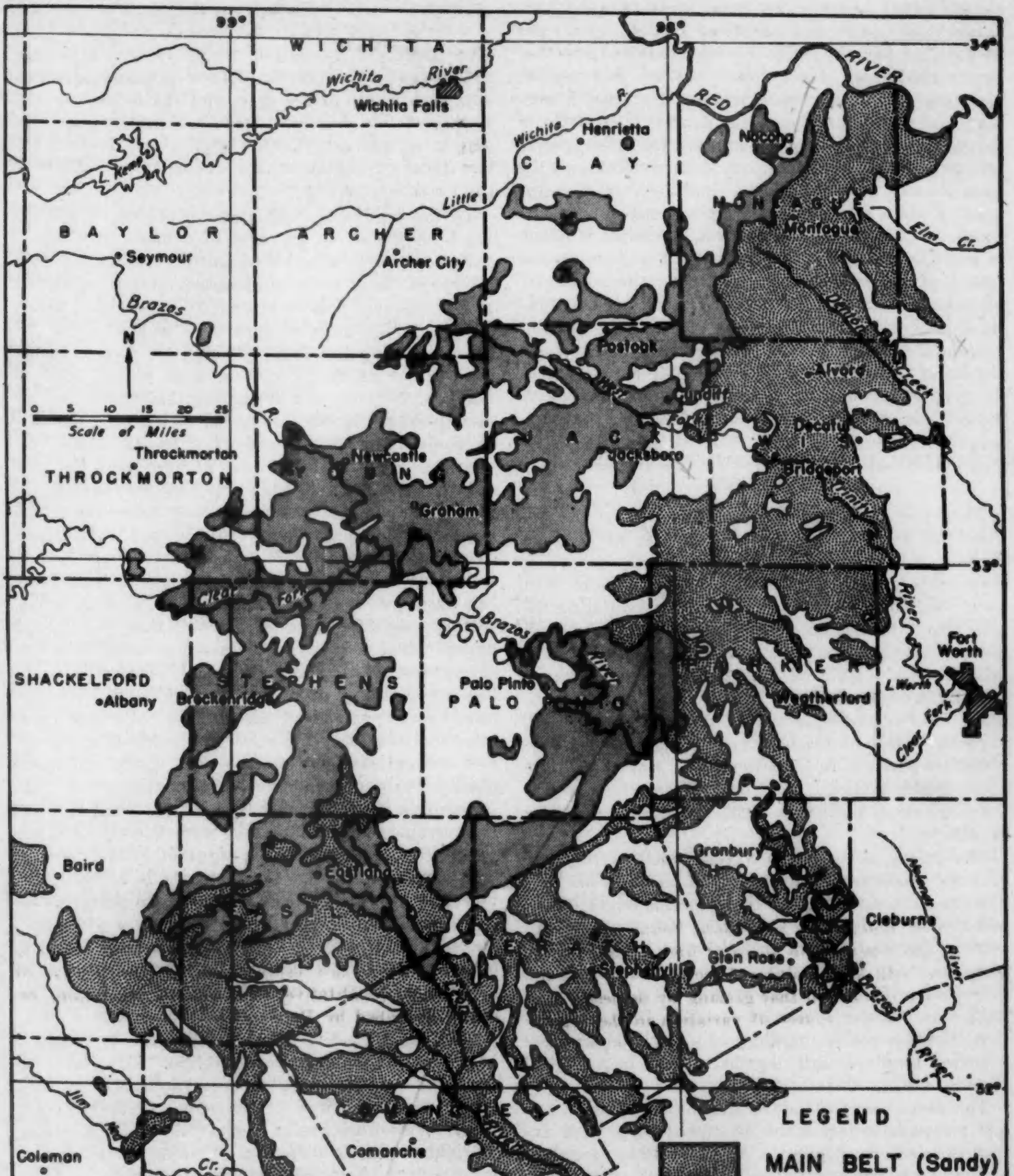


FIG. 1. Map showing location and boundaries of the Western Cross Timbers and its two major divisions. Both Main Belt and Fringe are characterized by a sparse overstory of post oak *(Quercus stellata)* and blackjack oak *(Quercus marilandica)*. Unstippled portions of the map were once open grassland but parts have now been invaded by trees other than oaks. The symbol "X" shows areas where stands of oaks were killed by the great drought of the 1930's.

clusively that edaphic factors resident in soils, particularly those affecting supply of available water are responsible for the relatively sharp boundaries between the major vegetation types of this region. McBryde has also described both overstory and understory vegetation of the forest nearest to the Cross Timbers, thus providing opportunity for making comparisons and contrasts between this savannah and the most closely related forest. Smith (1940) monographed biotic and physiographic succession on abandoned fields in central Oklahoma including portions of the Cross Timbers. He provided a comprehensive record of the changing fauna during the course of the subsere on abandoned fields. Osborn (1943) studied the wildlife of Young County, Texas, in relation to natural land types, including portions of the Western Cross Timbers. Dyksterhuis (1946) monographed the vegetation of the Fort Worth prairie which bounds this area on the east throughout its extent.

TIME, PURPOSES, AND METHODS OF STUDY

Field studies extended intermittently over the period 1938 to 1947, inclusive. The data on average floristic composition of the broad area are from cross-country transects taken in 1939. These data were found to be essentially correct by comparing results from additional transects in 1943. Data on seasonal development and grazing coactions were taken at the middle of each month from February 1944 to February 1945, inclusive. The data for February 1945 served as a check on data of the preceding year. Data on tracts of relict original vegetation were first obtained in 1938 and 1939. Such data were again taken in 1943, 1944, or 1945 on tracts where the vegetation meanwhile had remained essentially unchanged.

The principal species and their relative coverage over the broad area first were determined. This provided the average from which deviations might be observed and evaluated. Deviations found to be important and recurring in space or time included those associated with soils, history of use, and time of year. It was soon discovered that grazing by domestic livestock was a major source of variation in the vegetation. For this reason, grazing coactions received more attention than ordinarily has been given in ecological studies of local areas of vegetation.

The purposes of the study were: (a) To determine and record boundaries and area; (b) to provide future research workers with a quantitative record of ordinary present-day vegetation, and of such relicts or original vegetation as remained; (c) to determine the nature of major deviations from average floristic composition and the habitat factors with which they were associated; (d) to determine local indicators of degrees of degeneration of range land by sites, as a basis for corrective measures; (e) to determine coactions between grazing animals and plants by monthly observations of the former and autecological studies of the latter as means of contributing to knowledge of basic causes for range degeneration and regeneration; (f) to determine the course of the subsere on the vast acreage of formerly cultivated lands when ungrazed, grazed, or seeded to climax grasses; (g) to determine features of the vegetation associated with each month of the year; and (h) to provide contemporary technicians in land use and management with a reference to locally applicable literature and the status of our knowledge of the plant ecology of the Cross Timbers.

In the analyses of the vegetation major reliance has been placed on averages of mechanically spaced sample plots. Estimates of composition of the vegetation occurring under a given complex of influences are in all instances averages of impartially drawn samples. The type of plot used was a circle containing 100 square feet. Briefly, the data recorded were a list of the species of seed plants, and the number of square feet of surface that would be completely shaded by the foliage of each within five feet of the surface at the end of a normal year's unmolested growth. This type of plot and the procedure in its use have been described by Stewart and Hutchings (1936). Coverage was recorded to the nearest 0.25 square foot. Species not individually occupying 0.25 square foot per 100 were grouped in an appropriate category. It is recognized that absolute "amount of surface occupied" by a plant is subject to wide differences in interpretation even though an individual or party of trained men can obtain consistent results in measurements of relative amounts. The unreliability of estimates of absolute coverage have been reported by Smith (1944). For these reasons, and also to provide for summarization and direct comparison between different study areas, the absolute values were reduced to relative ones. The square-foot value for each species was computed for an average plot. From this were derived the percentages of total coverage assignable to each species. This percentage value for a species is hereafter referred to as coverage and may be defined simply as the relative amount of surface occupied by a given species in a specific area. Coverage has been found to be one of the most useful of five distinct ways of expressing quantitative relations of vegetation, recently described by Bauer (1943).

The first objective of the study was to obtain a broad picture of average vegetation. To obtain this estimate, lines of plots (transects) were run from boundary to boundary of the upper Clear Fork and upper West Fork basins of the Trinity River system at right angles to direction of major drainage, thus averting the effects of purely local edaphic or biotic influences upon the sample. Prior to field work, the transects were spaced on a map showing only major drainage and boundary, thus precluding bias in their location. The only deviations from the lines as originally drawn were where lines were later found to fall on or closely parallel to a road. Then an offset of one-eighth mile was taken. Lines paralleled each other with a seven-mile interval on the Clear Fork basin and a 12-mile interval on the West Fork basin. Direction in the field was maintained by compass and

distances were measured by pacing with the aid of a mechanical tally register. Plots were taken at 350-yard intervals and when this distance had been measured, the point reached was accepted as the center of the plot irrespective of the examiner's opinion as to representativeness of the vegetation. In other words, after the boundaries of the study area were established sampling was unbiased. A total of 76.5 miles of line were thus traversed in obtaining a sample of present-day average vegetation of the broad area.

At each plot, data were taken on coverage, physiognomic type, soil, slope, and erosion. Thus it was possible later to segregate the individual plot records upon any one of these bases and determine associated differences. When the principal variations in the vegetation of the broad area were known and classified, the individual plot records falling within each classification were averaged. These samples of average vegetation for each type have since been checked as adequate to reflect real differences by use of 232 additional mechanically spaced plots.

On areas of relict vegetation, plots also were read along straight lines at fixed intervals. The intervals varied according to size and shape of the area. The number of plots taken in each was such that the averaging in of additional plots had little effect on average relative-coverage values. In selecting relicts the writer has been guided by the concepts of Clements (1934, 1936). Relicts of original vegetation sampled in 1938 and 1939 had changed but little, with two exceptions, when revisited in 1943, 1944 or 1945. Data from the six most stable and representative tracts are given. All had been protected from grazing for ten or more years and had evidently never been subjected to destructive grazing. None had ever been subjected to cultivation, or clearing. Those on sandy soils supported scattered veteran post oak trees. Ring counts verified that they had been present prior to settlement of the area. All but two areas had been burned over at least once during the preceding decade, and a tract near the village of Cundiff had been burned annually in January for many years.

Data relating to seasonal developments were obtained by field work at the middle of each month on six tracts betwen Decatur and Alvord, Texas. These tracts were selected to represent the most common soil conditions of the Main Belt. At each monthly visit the grazing preferences of three herds of cattle of all ages were recorded. The ranges on which the three herds grazed were roughly equal insofar as potential productivity is concerned. One tract was heavily stocked, one moderately stocked, and one lightly stocked. All three ranges contained both uncleared areas and abandoned croplands intimately intermingled so that the cattle drifted at will from one type to another.

One of the six areas visited each month had been wholly protected from grazing for many years and contained a good representation of the principal species on a uniform slope of Windthorst fine sandy loam soil. On this tract specimens of 16 important perennial grasses were collected each month. The specimens are complete with weathered leaves up to three years old, and new leaves, rhizomes, stolons, tillers, shallow roots, and current, as well as old, flowering culms. Each month the specimen of each species was collected to be comparable to the specimen of that species collected a month earlier, differing only in being a month more advanced. These were dried and mounted and portions green at the time of collection remained green. The series of 12 for each species thus show characteristic appearance and stage of root and shoot development for each month in the year. The material has served to answer many questions that were not anticipated when the work was begun. Of special interest are comparisons between inherent characteristics of the species. For example, evidence of leaching as shown by monthly losses of autumnal color during the winter and spring, time of tillering, time of rhizome elongation, period of dormancy, time of maximum growth, and time of flowering. Inasmuch as this type of herbarium material is of obvious value to ecologists and range technicians, as well as to taxonomists and others, and has apparently not been described before, the writer suggests the name "autecological herbarium." The name would apply to series of dried plant specimens showing the annual cycle of variation within the individual species of a natural plant community within a specific set of environmental conditions.

Supplementing the preceding data on seasonal development of the important grasses, monthly notes were taken on other characteristic species. These notes included time of germination, flowering, and grazing.

Data on the subsere of formerly cultivated fields and on degeneration of rangeland were obtained by taking records on numerous tracts, the history of which had been observed, or could be ascertained from local residents. Much data on subseres, as well as general knowledge of the Cross Timbers, have resulted from the author's regular work in range conservation. In presenting the data on subseres and degeneration, the results were reduced to photographing selected areas representing typical "stages" or conditions that are readily distinguished by the layman and then recording composition of the vegetation at the selected locations only.

The area is quite inadequately served by any one flora. In fact, it appears not to have been very thoroughly botanized. The author encountered numerous species beyond their published range in Texas, as well as a few species not previously collected in the state. Specimens of doubtful identity or evidently new to the state were mailed to specialists. Geiser (1937) has published maps showing areas in which frontier plant collectors worked. These aided greatly in determining that such widely known Texas field botanists as Berlandier, Drummond, Lindheimer, Roemer, and Wright did not botanize in the Western Cross Timbers. The works of Gray (1888), Small (1903), Hitchcock (1935), Stemen and Meyers (1937), Cory and Parks (1938), and Lundell *et al*

(1942, 1943, 1944) have been most helpful. The use of some one standard by which to resolve synonymy in both common and scientific names insofar as possible was believed advisable. For this reason, names used, with few exceptions, are taken from Standardized Plant Names, 2nd edition, Kelsey and Dayton (1942). Authority names are given with scientific names of species that were not listed in this work, and also in cases where the species intended might otherwise be in doubt. A few common names have been supplied by the author where standardized common names were not available.

EARLY ACCOUNTS OF VEGETATION

The Cross Timbers is probably mentioned more often, in written accounts of early southwestern travelers, than is any other vegetation type. The writer has endeavored to locate the earliest and the most informative accounts but there can be no assurance that all of the numerous accounts have been considered. The reason for this prominence in the literature may be surmised from Kennedy's (1841) account, previously quoted. The numerous early references have been consulted in an effort to obtain a more intimate knowledge of the original vegetation. Since the Western Cross Timbers is now largely range land or native pasture, most woody species are undesirable because of unsuitableness as forage and because of competition with herbaceous species. Much interest centers around consideration of the relative amounts of herbaceous and woody vegetation prior to settlement and now. If the grasses were originally predominant and the forest savannah-like, this condition could be restored by clearing and could then possibly be maintained rather simply by not overgrazing the understory. On the other hand, if the Cross Timbers was originally forest or a jungle of trees and woody vines, then the fight against woody invaders would have to be a constant one. It would then be clear that the climate in conjunction with these soils tended always to favor woody vegetation even though the grasses were not prevented from competing effectively by grazing. If woody species were originally dominant, proper stocking with livestock could only result in natural succession leading to dominance of woody species rather than grasses. If savannah were the original condition, then the possible role of prairie fires in maintaining this condition must also be evaluated since most ranges are no longer burned.

The earliest reference to the Cross Timbers encountered was dated July 4, 1772, and is provided by Bolton (1914) in the translation of a report by De Mezieres to the Baron De Ripperda on the expedition of 1772. De Mezieres stated, "Two leagues southeast from here begins the Monte Grande (Big Forest) called Galvan, which extends to the east-northeast. Since it contains some large hills, and because of the great quantity of oaks, walnuts, and other large trees, it is a place difficult to cross. . . . On the farther edge of this range, or forest, one crosses plains having plentiful pasturage. . . ." In a letter to Croix concerning the expedition of 1778, dated April 18, 1778, De Mezieres stated that from the Brazos River north ". . . one sees on the right a forest that the native appropriately call the Grand Forest. It seems to be there as a guide even to the most inexperienced, and to give refuge in this dangerous region to those who, few in number and lacking in courage, wish to go from one (Indian) village to another." Bolton (1914) regards the last reference as applying specifically to the Eastern Cross Timbers. It is of interest that the name Grand is now applied only to the belt of prairie between the two belts of "Cross Timbers."

Bolton (1915) has reproduced an original map dated 1789 of the route of Vial and Fragosa from Santa Fe to Natchitoches in 1788. From this map it is clear that Vial and Fragosa successively crossed the Western Cross Timbers, the Fort Worth Prairie, and the Eastern Cross Timbers. The Western Cross Timbers is correctly illustrated as wider, less continuous, and with more rugged relief than the Eastern Cross Timbers. This is evidently the earliest map of record.

Ellsworth's journal of a trip in 1832 (Williams and Simison, 1937) stated, "Before we started, Col. Arbuckle told us many frightful stories about the cross timbers and we expected more difficulties than we found . . . it is a mixture of wood & small prairies. . . . The fires of the Prairies, extend through the cross timbers, and the skrubby oak, whose branches are proverbially tough, naturally, become doubly so, by being burnt. . . . I never saw a man more impatient, to be out of them, than Mr. Irving. While, he was passing through what he called the cast iron stuff, protecting his head, & eyes, and cap (which was knocked off several times every day) the whole of one skirt of his coat was taken off . . . although travellers *have* & *will* decry this land, yet, I am confident it will be found tolerable pasturage, for sheep & cattle besides yielding an inexhaustible supply of wood & timber when the prairies shall not be burnt. . . . Capt. Bean says 'he had quite as lives travel in these woods as on the dry open prairie.' I am not of this opinion but the obstacles we met with, were far inferior to travelling on any point of compass in Connecticut without roads. . . ."

This account refers to the area now roughly located between Oklahoma City and Tulsa, Oklahoma. Ellsworth refers to Washington Irving who accompanied him and who also gives a colorful account of the Cross Timbers in his "A Trip Upon the Prairies."

Col. Stiff (1840) who approached the Cross Timbers of Texas from the western prairies stated, "In turning to the northeast, something much resembling an irregular cloud is dimly seen. This is a skirt of woodland . . . called the Cross Timbers. . . . Whether this was once the beach of a mighty lake or sea we must leave to the geologist to determine."

A copy of a map provided by Fulton (1941) shows that Josiah Gregg had a sketch map of the Cross Timbers north of the Red River as early as 1839 or 1840. Gregg's diary of April 7, 1840, states: "These

cross-timbers are dismal, roughly grown up with various kinds of undergrowth, grapevines, green briars, etc., all so thickly matted that man or beast can scarcely pass through them without a road. Should our frontier Indians engage in war again with the U. S. I fear these cross-timbers will afford them a hiding place and shelter as formidable as the swamps of Florida." This account applies to an area in east-central Oklahoma receiving approximately 38 inches of average annual precipitation. This is six inches more than the most received in the Western Cross Timbers of Texas.

Kendall (1845) stated that on July 21, 1841, "We were now fairly within the limits of the Cross Timbers. . . . The immense western prairies are bordered, for hundreds of miles on their eastern side, by a narrow belt of forest land, well known to hunters and trappers under the above name." Kendall had entered the Western Cross Timbers near its southern extremity and had found it extremely difficult to traverse with wagons because of the gullies and the undergrowth. He stated, "The growth of timber is principally small gnarled, post oaks and black jacks, and in many places the traveller will find an almost impenetrable undergrowth of brier and other thorny bushes."

Marcy (1849), traveling eastward, stated in his diary of October 29, 1849, "We have been passing near the borders of the 'Upper Cross Timbers' all day, and gradually approaching them until we are within a mile. We have seen but little mezquite timber today, and the mezquite and grama grasses have almost entirely disappeared; but we find the other kinds of prairie grass in abundance." (Here Marcy evidently refers to the ecotone between short and mid grasses of Mixed Prairie and the mid and tall Andropogons of the True Prairie.)

On October 31 he wrote, "We passed through the 'Upper Cross Timbers' to-day and encamped upon an affluent of the Trinity. . . . The soil through the Timbers is more sandy than it has been further west, but there are many small glades where the soil is good and well adapted to agriculture."

Hill (1887) stated, "The absence of fertilizing ingredients in the Upper Timbers also accounts for the exceedingly scrubby growth of timber, which peculiarity, however, the inhabitants always ascribe to the burning of the adjacent prairies."

The foregoing accounts make it clear that scrubby oaks have long characterized the landscape and that some gullies occurred in the Cross Timbers prior to settlement. Furthermore Marcy's diary (1849) shows that the dominant grasses of the Western Cross Timbers were originally different from those on the area adjacent westward. It also indicates that mesquite *(Prosopis juliflora)* had not yet invaded the Western Cross Timbers. The reports are conflicting with respect to amount of woody vegetation. Later Marcy (1866), who had evidently determined that this matter required clarification, summarized his 30 years of travel by stating of the Cross Timbers, "At six different points where I have passed through it, I have found it characterized by the same peculiarities; the trees, consisting principally of post-oak and black-jack, standing at such intervals that wagons can without difficulty pass between them in any direction. The soil is thin, sandy, and poorly watered." Nonetheless, certain portions in Oklahoma with relatively high rainfall and others with especially favorable moisture relations, such as Nimrod sands, may have supported dense woods. Furthermore, dense thickets of saw greenbrier *(Smilax bonanox)* are common today on localized areas of deep sands.

Marcy's (1866) statement is in accord with accounts of numerous early settlers of the Western Cross Timbers who have been personally interviewed. Such old settlers usually state that the worst drought of memory occurred in 1886 and 1887. They recall that before this time a large coarse grass was abundant in the bottoms, and that another of medium height was abundant on the slopes and ridges. Both, they say, were replaced by other shorter grasses and weeds in 1886 and 1887 and have never been common since. They attribute the disappearance of the taller grasses solely to drought, but admit that grazing was already intensive at that time and has continued until the present. Also, it should not be overlooked that at this time the "patch" farmers were settling in the country and burning of range land was largely discontinued almost simultaneously. Thus four separate influences may have been partially responsible for placing the invading plants in a more favorable position. These were: intensive grazing by domestic livestock, cultivation of areas which could serve as sources of seeds of numerous invading plants, cessation of extensive prairie fires, and great droughts.

The oldest ranchers in the western portion, in speaking of their earliest impressions, and from information obtained from others, state that the Cross Timbers fringe had no undergrowth of shrubs and that tall grasses grew luxuriantly in the woodland as well as in the openings. They recall that fires in the tall grasses were common during dry periods, and that these tall grasses when afire, burned the limbs off the trees to a height that enabled a man on horseback to ride beneath their crowns. They state that when the first white settlers from more easterly locations arrived, the Indians regularly burned off the grass and had done so for years. The first settlers, principally ranchers, took up the practice and continued it until "patch" farmers entered the scene, and improvements erected by them, such as rail fences and log buildings, made promiscuous burning too hazardous. One of the first ranchers in the vicinity made the following comment: "I wouldn't know, but I have heard that the Spanish who were in this country long before us taught the Indians to burn off the grass. I have heard that the Spanish burned off their pastures in this country to get rid of 'varmints' and bushes."

DESCRIPTION OF AREA

Climate

The Western Cross Timbers fall within the moist-subhumid-mesothermal climate described by Thornthwaite (1931, 1941). In ordinary years rainfall slightly exceeds evaporation and the needs of plants. Therefore, the subsoil is generally moist. Accretion to ground water, and some run-off may be expected even under climax vegetation. Percolation of rain-water to depths greater than those reached by the roots of plants has permitted soluble soil materials to be leached to great depths. The region of dry-subhumid climate adjoins this area on the west.

Isohyets as mapped in the U. S. Department of Agriculture Yearbook, Climate and Man (1941), show that average annual precipitation increases from west to east, being about 26 inches in the western part and 32 inches in the eastern part. Most of the Fringe receives 26 to 28 inches while the Main Belt receives 28 to 32 inches except at the extreme westward extension near Baird where average annual precipitation may be no more than 24 inches. April and May are the months of greatest precipitation. November, December, and January are the months of least precipitation but drought as reflected by amount of soil moisture and appearance of the vegetation is usually most marked in July and August and sometimes continues well into September. The average date of the last killing frost in spring varies from about March 20 to March 25 depending upon location. The average date of the first killing frost in autumn varies from about November 5 to November 15 depending upon location. Maximum temperatures have exceeded 110° F. during the ordinarily hot and dry July and August, while minimum temperatures have dropped a few degrees below zero in January which is usually the coldest month. However, periods of freezing temperatures usually are maintained for only a few days at a time and the infrequent light blankets of snow soon disappear. Average annual snowfall varies from about 4 inches at the north to 2 inches at the south. Average depth of frost penetration varies from about 6 inches at the northern extremity to 3 inches at the southern extremity.

Geology

The very existence of the Cross Timbers is largely traceable to certain geologic units from which the sandy soils are derived. Geologists have confirmed Colonel Stiff's (1840) early surmise that the Western Cross Timbers marked what was once the beach of a mighty sea. This sea of Cretaceous times in its general retreat to the east and south to the present Gulf of Mexico left "beaches" alternately of arenaceous and calcareous materials. These today are characterized by savannah or forest, and grassland, respectively. Thus, in its retreat it left arenaceous materials (Western Cross Timbers), calcareous materials (Fort Worth Prairie), arenaceous materials (Eastern Cross Timbers), and other marine deposits originally laid down upon the marginal bottoms of a sea which in its general retreat also at times advanced.

Hill (1887) first stated that the position of the Cross Timbers was adapted to geologic formations, being upon outcrops of certain arenaceous formations of Cretaceous rocks and with deep permeable regolith and sandy soils which favored tree growth. These he contrasted with the close-textured calcareous soils of the treeless intervening prairie. Hill (1901) also pointed out that the eastern portion only of the Western Cross Timbers is upon Cretaceous outcrop and referred to this portion as the "main belt." For this reason the author has retained the name "Main Belt" for the Cretaceous portion, which also has a distinctive flora. Hill (1901) mentioned the Main Belt as facing the scarp of the Grand Prairie (Fig. 2).

Of the Western portion Hill stated, "Sometimes it is sharp and definite, while again it merges into local forest areas occupying other arenaceous formations than those of the Cretaceous." The others referred to are Pennsylvanian formations. An excellent map of the boundary between outcrops of Pennsylvanian and Cretaceous strata within the area of the Western Cross Timbers is given by Scott and Armstrong (1932). A distinction between the two areas is made by referring to the former as Fringe and the latter as Main Belt. Even though oaks may be found upon uplands of both, the understory vegetation and soils show differences to be described.

Cuyler (1931), who studied vegetation as an indicator of Cretaceous formations in Texas, found that Pennsylvanian-Cretaceous contacts in this area were commonly distinctly marked by post oaks and blackjack oaks on the Cretaceous side of the contact. Bullard and Cuyler (1930) had previously noted that some of the sandstones of the upper Pennsylvanian lying to the west of, or protruding through the Cretaceous, produced very rugged, hilly topography, also supporting a thick growth of oak timber (Fig. 3).

Sellards, Atkins, and Plummer (1932) in describing the Trinity group of the Comanche (Lower Cretaceous) series of Cretaceous units in Texas stated, "The Trinity group in its northern, more sandy facies forms the Western Cross Timbers." They point out that sediments of this group were deposited in a transgressing sea whose margin moved northward in Trinity time and that practically everywhere its base consists of sand or conglomerate.

Soils

As mapped and described by the U. S. Department of Agriculture, Bureau of Chemistry and Soils (1938), the soils of the main belt of the Western Cross Timbers belong to the Windthorst-Nimrod Soil Association of Zonal Red and Yellow Podzolic soils. The "included prairies" of the western portion belong to the Zaneis-Renfro Soil Association of Zonal Reddish Prairie soils.

This broad classification is admirably suited to correlation with the physiognomy and composition of the vegetation provided two other soil categories are admitted. One is an Azonal category that may be called Immature Reddish Prairie, found primarily in the western and driest portion. The other is an In-

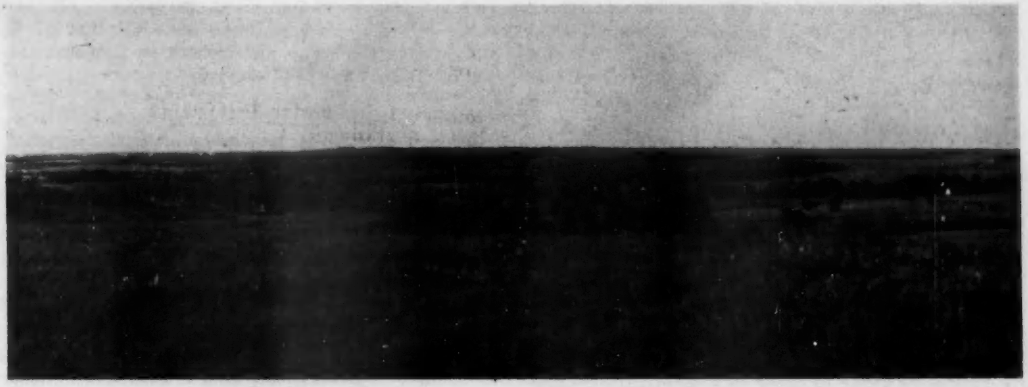


FIG. 2. View at the eastern edge of the Western Cross Timbers, facing N. 20° E, at Decatur, Texas. At the right is the scarp of the Fort Worth prairie with greater elevation and open grassland which faces the oak woodland and cleared fields of the Cross Timbers on the left. The limestones of the prairie have been more resistant to geologic erosion than the sandstones of the Cross Timbers and hence have greater elevation today, even though when first exposed by the retreating sea of Cretaceous times the surface of the prairie was lower. This accounts for the evident anomaly of streams from the Cross Timbers flowing eastward through the higher prairie country. Valleys today are wide with gentle slopes within the Cross Timbers but where they cross the prairie they are narrow and deeply entrenched. The limestones have weathered to form clay soils with a climax of mid grasses, whereas the sandstone of the Cross Timbers formed fine sandy loam soils. The superior water relations of the sandy soils permit growth of oaks which are postclimax in this grassland climate.

trazonal category consisting of Rendzina soils that occur locally within the boundaries of the Cross Timbers. The vegetation and soils of the Intrazonal Rendzina category are similar to those of the Fort Worth Prairie described by Dyksterhuis (1946).

The soils that will be referred to as Immature Reddish Prairie soils are now commonly mapped as Reddish Prairie soil materials. They occupy the areas of greatest relief. Rocks are found in and on the soil. The areas commonly take the form of ridges locally called "mountains" and these border on flats with mature Reddish Prairie soils. The oaks occur naturally on the immature soils but seldom occur on the flats except where intensive grazing has favored them in competition with grasses. The controversial problem of the causes for the prairie-timber transition on apparently similar soils as ably reviewed by Jenny (1941) is not applicable. The soils on which the oaks occur naturally here are obviously more permeable. McComb and Loomis (1944) have shown that where

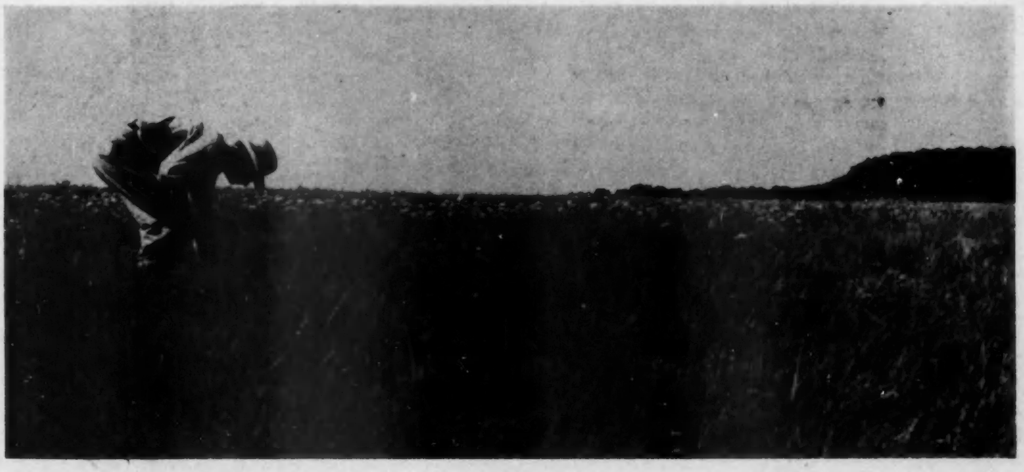


FIG. 3. View at the western edge of the Western Cross Timbers. A portion of the Fringe is shown in the right background where the oaks occupy rugged relief of sandstones of Pennsylvanian age. The Fringe is bordered on the west by Reddish Prairie soils of gentle relief. Range in excellent condition on Reddish Prairie soils is shown in the foreground. *Andropogon scoparius* and *Sorghastrum nutans* are dominant. *(Photo. by Mack McConnell.)*

climate approaches that of a prairie climax, forest potentialities are limited to the coarser-textured, better aerated soils. The better moisture relations and consequent ability of porous soils to support trees even though in a grassland climate has been emphasized by Clements (1916).

Mechanical analyses of typical Windthorst fine sandy loam were reported by Bushnell, Hawker, and Pratapas (1923). They found that clay comprised only 4.5 percent of the surface soil but 33.8 percent of the subsurface and 28.7 percent of the subsoil. Fine sand and very fine sand together comprised 79.0 percent of the surface soil. They pointed out that inasmuch as the soil material is a mixture of sand and clay the processes of soil formation must have translocated a large part of the fine material to the deeper horizons in order to develop mature profiles of the type described. A representative profile is shown in Figure 4.

Chemical analyses of surface soils and subsoils of the Western Cross Timbers have been reported in detail by Fraps and Fudge (1937). They found all rolling upland prairie soils very deficient in active phosphoric acid. Virgin profiles of the most common soil type, namely, Windthorst fine sandy loam, had averages of 0.050 percent of nitrogen in the surface soil and 0.049 percent in the subsoil. The average pH of surface soil was 6.9 while that of the subsoil was 6.6. The pH of both surface and subsoil of Nimrod fine sand was 6.6.

Grazing Influences

Though grazing is largely on natural vegetation, to be described, there are some permanent tame pastures. Bermudagrass *(Cynodon dactylon)* is used, almost exclusively, as the base grass for such pastures. It is more exacting in moisture requirements than the native grasses of uplands. Its usefulness appears limited to alluvium and possibly to well fertilized Nimrod fine sands and other fertile soils of exceptionally favorable moisture relations. On such sites it is able to increase under grazing whereas on all ordinary uplands, where it has been tried, it fails to increase its coverage or to provide any significant amount of pasturage. The poor growth on uplands is undoubtedly due in part to low soil fertility, and research is badly needed (Fig. 5).

Johnsongrass *(Sorghum halepense)*, though widely escaped and useful as temporary tame pasture, does not persist under the close and continuous grazing to which it is ordinarily subjected. Under such grazing use it is commonly perpetuated by an occasional

Fig. 4. A profile of typical Windthorst fine sandy loam which is the predominant soil type of the Main Belt of the Cross Timbers. The surface soil is medium-textured, light brownish gray, fine sandy loam or sandy loam, of single grain structure. It grades abruptly into red subsoil of compact clay or fine sandy clay that is slowly permeable. When dry this layer separates into irregular angular fragments. The subsoil grades into weakly cemented sandstones. The profile is non-calcareous. *(Photo. by R. W. Hufnagle.)*

cultivation. Where protected from grazing, Johnsongrass persists among climax grasses for many years. Bermudagrass does not.

Local areas of native vegetation within the Cross Timbers were probably overstocked with cattle prior to 1800. Bolton (1914) provides the translation of a letter from De Mezieres to Croix, dated March 18, 1778, concerning an expedition to the Indian nations of the Upper Trinity, Brazos, and Red Rivers. De Mezieres stated, ". . . I crossed the Colorado and Brazos, where there are . . . an incredible number of Castilian cattle, and herds of mustangs that never leave the banks of these streams. The region from one river to the other, is no less bountifully supplied with buffalo, bear, deer, antelopes, wild boars, partridges, and turkeys."

The average stocking rate has declined tremendously since native ranges were first fenced and heavily stocked. This occurred in the 1870's and 1880's about a century after De Mezieres' report. A half century ago Smith (1899) submitted questionnaires to ranchers asking their opinion of grazing capacity and of estimated percentage increase or decrease during the preceding 25 years. His replies from representative counties of the Cross Timbers indicate that 6 to 10 acres were provided for each cow for year-round grazing. All counties reported decreases from earlier grazing capacities. These decreases ranged from 30 to 50 percent. Today stocking rates on representative ranches range from 12 to 20 or more acres per cow year-round or equivalent. Though stocking rates vary from ranch to ranch and on the same ranch from year to year it appears that native pastures of the Cross Timbers during the past decade have been stocked at an average rate of about 14 acres per cow year-round or equivalent. Bonnen and Thibodeaux (1937) report an average carrying capacity of 15 acres. Farm pastures of native species are usually stocked much more heavily than ranch pastures and show proportionately greater prevalence of annuals and nonpalatable perennials. The rates at which pastures have been stocked are scarcely indicative of actual grazing capacity because degeneration of the range land provides abundant evidence that the grazing capacity has been greatly exceeded.

FIG. 5. Bottomland subject to frequent overflow that has been converted to a tame pasture of the introduced Bermudagrass *(Cynodon dactylon)*. Trees have been cleared excepting pecan. Frequent mowing is necessary to control encroachment of other plants. Bermudagrass is the only common perennial base grass of tame pastures and is widely escaped. It did not encroach upon the area above overflow shown in the background where annual species of Aristida predominated.

WOODLAND OVERSTORY AND FORESTRY

Timber of saw-log size is now found only on the flood plains of streams. Many flood plains are now choked with tremendous quantities of silt and almost sterile sands which might be stabilized by reforestation and protection from grazing (Fig. 6). Very rough construction lumber was once cut from virgin upland post oak where it attained its maximum size on deep sands. On such sites dominant native trees are now usually about 12 inches in diameter but over-mature specimens may attain 16 inches in diameter at breast height. Clear length seldom exceeds eight to ten feet. Total height is 30 to 45 feet.

FIG. 6. Vast quantities of silt and almost sterile sands are eroded from fields and overgrazed uplands. Deposition in drainages, as shown, periodically destroys natural vegetation, croplands, reservoirs, roads, and fences. Eroded uplands and choked channels result in abnormal flood hazards.

According to a U. S. Department of Agriculture Flood Control Survey (1942), woody vegetation occupied about 35 percent of the land surface of the Main Belt. The woody overstory consisted of the following: 63 percent post oak *(Quercus stellata)*, 29 percent blackjack oak *(Quercus marilandica)*, and 8 percent composed of some ten other species most common among which were cedar elm *(Ulmus crassifolia)* and hackberry (*Celtis* spp). The average density of the crown canopy is given as approximately 55 percent within uncleared areas. Data from 269 one-quarter acre sample plots in stands of the Main Belt near the eastern margin which supports the best tree growth, indicated that there was an average of about 362 stems per acre over 1.1 inches in diameter at breast height. Of these, 10 percent were dead, 20 percent diseased, and 16 percent fire-scarred. Of the total, 27 percent were judged defective even for eventual production of fence posts. None of the 269 plots fell in old growth stands, 98 percent fell in

second growth stands of sprout origin, and only 2 percent fell in stands possibly originating from seed, since settlement. Since spacial distributions of trees over the landscape in a measure describes the aspect of the forest or savannah, it is of interest that 69 percent of the area had trees evenly distributed, 17 percent had trees in clumps and 14 percent had scattered trees. Average depth of tree leaf litter over the entire area was reported as about one-third inch.

The annual increment of wood per acre on existing woodland was given as 9.50 cubic feet per acre for the Western Cross Timbers Fringe and 10.84 cubic feet for the Main Belt. It was estimated that with fully stocked stands and good forest management these values could be approximately doubled.

Wood cutting is common but forestry as such has not been encountered except on bottomlands where an occasional portable sawmill may be found. Considerable quantities of upland oak are cut each year for fuel and some for fence posts. However, such cutting is usually done with at least the partial objective of clearing the land for better grazing or other uses. Ranchers commonly have commercial wood cutters clear areas of woody vegetation, charging nothing for wood products removed. In other cases, small trees are felled and large trees are girdled as a means of range improvement without any salvage of wood (Fig. 7).

FIG. 7. Post oak and blackjack oak were cut or girdled five years earlier. All trees over 10 inches in diameter were girdled and small trees were cut 2 to 3 feet above the ground. No wood was salvaged. The purpose of clearing was to improve the area as range for cattle. No sheep or cattle were permitted on the area while the oak sprouts were being "goated." Numbers of goats per acre were such that sprouts were completely defoliated within relatively short periods after which the goats were removed until new leaves appeared. At the end of the three years most of the oaks had been killed. The area was then protected from all grazing for 2 years during which the cover of principally *Andropogon scoparius* and *Sorghastrum nutans* attained the density shown. The cleared hills in the background were still eroding.

FIRE

In speaking of earliest impressions of the vicinity of Jacksboro early settlers recall no undergrowth of shrubs but rather mid and tall grasses through which fires commonly burned in dry periods. They stated that these fires burned the low bushes and also the lower limbs off the trees to such height as enabled a man on horseback to ride beneath their crowns. Fires are now uncommon in this Fringe area. This may well explain why the oldest trees today have a clear though short bole, while younger trees of the same diameter and upper crown characteristics are commonly branched to the ground.

In the Main Belt of the Western Cross Timbers fires are still rather common, but on any one tract, fire is usually periodic rather than annual. A survey report of the Trinity River watershed by the U. S. Department of Agriculture (1942) described frequency of fires, primarily from ring counts on burn scars found, on 269 sample plots. The report states that 16 percent of the area had not been burned for 10 years or more, 37 percent had not been burned for 6 to 9 years, 44 percent had not been burned for 1 to 5 years and 3 percent had been burned during the preceding year.

Elwell, Daniel, and Fenton (1941) investigated effects of burning on rate of erosion and runoff in the Cross Timbers of Oklahoma. They found that average annual soil and water losses were increased 12 and 31 times, respectively, as a result of burning.

CULTIVATION AND CROPS

Very little of the rocky and gravelly fringe portion of the Western Cross Timbers is farmed. Cultivation in this area is largely confined to the "included prairies" or flats (Fig. 8). Such flats are usually devoted to small grains, Johnsongrass, or grain sorghums which provide supplementary tame pasture and feed for range livestock.

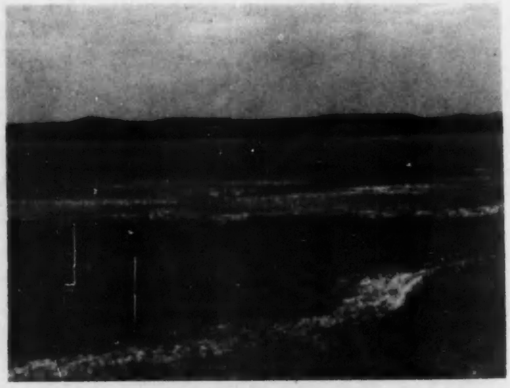


FIG. 8. A typical "flat" or "included prairie" of the Western Cross Timbers is shown in the foreground. Rugged hills or "mountains" covered with oaks are shown in the background. The flats were once open grassland but are now commonly cultivated to provide winter feed for livestock that range in the hills. Uncultivated flats are invaded by mesquite *(Prosopis juliflora)*.

The Main Belt with its gentle relief and sandy soils is used for production of various cash crops including fruits and vegetables. Current land use in the Main Belt was calculated from data by the U. S. Bureau of Agricultural Economics and the Texas Agricultural Experiment Station (1946). Summarily these data indicate that in 1945 about 17.8 percent of the area was in cultivation. Virtually all of the remainder supported native or volunteer vegetation and was used for grazing. Of the cultivated portion 70 percent was in intertilled crops and 30 percent was in close-growing crops. The principal crops and the amounts of the total cultivated area devoted to each were: peanuts, 34 percent; sorghums, principally grain sorghums, 16 percent; small grains, 20 percent; corn, 5 percent; cotton, 3 percent; sod crops or hay, 7 percent; all others, 5 percent.

EROSION AND CHANGING LAND USE

A distinctive characteristic of the Windthorst and Nimrod soils of the Cross Timbers is their extreme susceptibility to accelerated erosion under cultivation. Tremendous gullies are today associated with areas of Windthorst fine sandy loam whereas wind erosion is equally characteristic of deep sands particularly Nimrod fine sand (Figs. 9 and 10, respectively).

Subdivision of the large ranches into farms began near 1890 and continued for 20 to 40 years depending upon locality. The sandy upland soils soon lost their original fertility under cotton and corn production. These and other intertilled crops exposed the sandy surface soil to the elements through a large part of each year. The accumulated organic matter of centuries oxidized in less than a decade under such treatment. Soon severe erosion caused abandonment of many fields and whole farms. Bennett (1939) reported the degree to which land in different uses had eroded. Data on rates of erosion and deposition have been published in a U. S. Department of Agriculture Survey Report (1942).

FIG. 9. Gully erosion characteristic of the Main Belt. Huge gullies develop in fields and along roads. The exposed soil-parent-material is white, nearly sterile, weakly cemented sand of the Trinity group of Cretaceous strata upon which once rested a productive Windthorst fine sandy loam soil. Vegetation has not volunteered on the exposed parent material even though it has been protected from grazing for several years. Plants growing in the gully are those that have fallen from the edges carrying some soil with them.

Consolidation of small crop farms into livestock farms and ranches usually followed division of ranches into farms after only two to four decades of cultivation. In the western part about 14 percent of the area remains in cultivation and in the eastern part about 18 percent. Formerly cultivated lands, that are now virtually idle even as a source of pasturage, are characterized by gullies and annual threeawn grasses (*Aristida* spp.). Such abandoned fields of threeawn grasses occupy a surprising part of the total area. From sample farms on the Trinity River watershed (U. S. Department of Agriculture Survey Report, 1942) it was deduced that in the western part about 2.3 percent and in the eastern part about 9.2 percent of the total land area had been abandoned because of erosion. These figures are high in light of the small part of the total area that was ever cultivated.

Bonnen and Thibodeaux (1937) pointed out that before 1914 cotton occupied about two-thirds of the cultivated area whereas in 1937 it occupied only one-third. Meanwhile the acreage devoted to pasture, production of livestock, and livestock products had increased.

FIG. 10. Deep sands of the Cross Timbers, principally of the Nimrod series. Such sands are commonly associated with almost level relief and once supported the best stands of oak. Under cultivation and production of such clean-tilled crops as peanuts they have been severely eroded by wind. The topsoil is blown into fence rows and adjoining woodlands.

DISCLIMAX UNDERSTORY VEGETATION AND COVERAGE BY SPECIES

As stated by Clements (1936) and Weaver and Clements (1938), disclimax communities commonly result from modification or replacement of the true climax, either as a whole, as by cultivation, or in part, as a result of grazing. Apart from the original savannah-like overstory of oaks which constituted a postclimax in this prairie climate (Weaver and Clements, 1938) the understory was once essentially climax prairie vegetation.

The original understory vegetation has been greatly modified since settlement. Vegetation present today no longer reflects only climate and soil, but also response to grazing by domestic livestock. Since grazing has been largely poorly managed and destructive, the original vegetation has been displaced and the present vegetation may be termed simply disclimax, a product of disturbance.

The degree of grazing disturbance is best described by the effect that it has had in altering composition of the original or climax vegetation. In the following sections the disclimax vegetation is described, and compared with the original vegetation.

Average Vegetation of the Broad Area

The average relative coverage of the principal species was determined from 76.5 miles of cross-country transects with sample plots at one-fifth mile intervals. If an acre or other unit of surface were to have "average" present-day vegetation of the entire Western Cross Timbers, its composition would be approximately as indicated in Table 1.

Table 1 shows that the principal grass is buffalograss *(Buchloe dactyloides)*. Perennial grasses enumerated compose 41 percent of the total plant cover while annual grasses compose 16 percent. Annual grasses are slightly less abundant than annual forbs which compose 18.8 percent of the plant cover. Post oak and blackjack oak, together the dominant feature of the landscape, constitute 7.4 percent of total coverage of vegetation within 5 feet of the surface. Other woody plants, particularly saw greenbrier *(Smilax bonanox)*, and perennial forbs, especially western ragweed *(Ambrosia psilostachya)* account for the remainder.

In the understory the short grasses predominate with perennial mid grasses occupying only about 14 percent of the total coverage. Tall grasses were found, but only in trace amounts.

Table 1. The principal species of the Western Cross Timbers and their relative coverage.

Species or Groups: Common Name	Species or Groups: Scientific Name	Coverage
		Percent
Annual forbs		18.8
Buffalograss	Buchloe dactyloides	9.4
Post and Blackjack oaks	Quercus spp.	7.4
Annual threeawns	Aristida spp. (annual)	5.9
Hairy grama	Bouteloua hirsuta	4.6
Perennial threeawns	Aristida spp. (perennial)	4.0
Fringeleaf paspalum	Paspalum ciliatifolium	4.0
Texas stipa	Stipa leucotricha	4.0
Little barley	Hordeum pusillum	3.9
Sixweeks fescue	Festuca octoflora	3.5
Saw greenbrier	Smilax bonanox	3.1
Silver bluestem	Andropogon saccharoides	2.8
Sideoats grama	Bouteloua curtipendula	2.7
Bermudagrass	Cynodon dactylon (escaped)	2.4
Western ragweed	Ambrosia psilostachya	2.3
Annual bromes	Bromus spp. (annual)	2.2
Perennial forbs except ragweed		2.0
Tumblegrass	Schedonnardus paniculatus	1.8
Perennial lovegrasses	Eragrostis spp. (native)	1.6
Windmillgrass	Chloris verticillata	1.3
Common mesquite	Prosopis juliflora	0.9
Little bluestem	Andropogon scoparius	0.8
Skunkbush sumac	Rhus trilobata	0.8
Fall witchgrass	Leptoloma cognatum	0.7
Tall dropseed	Sporobolus asper and var's.	0.6
Mat sandbur	Cenchrus pauciflorus	0.6
Pricklypear	Opuntia spp. (flat-stemmed)	0.6
Scribner panicum	Panicum scribnerianum	0.5
All others*		6.8

*Species individually having less than 0.5 percent coverage.

Differences Between Main Belt and Fringe

The Western Cross Timbers varies but little in general appearance as one travels north and south through the Main Belt. However, the general aspect changes markedly within a distance of 50 miles in an east to west direction. As one travels from the Main Belt into the Western Fringe progressively lower stature of mature trees is noted. Also surface relief becomes more varied, changing from gently rolling in the Main Belt to rugged hills with intervening flats in the Fringe. Cultivated fields become less frequent, cacti and mesquite are observed and the whole suggests increasing aridity. Actually the difference in rainfall is small, being no more than 2 to 4 inches annually. However, effectiveness of equal amounts is less in the western part because of the higher clay content of the soils generally, and subsequent lesser infiltration of rainfall and lower percentages of soil-water available to plants. A comparison of the relative amounts of the various species in the Main Belt and Fringe portions is given in Table 2.

It may be noted from Table 2 that buffalograss, a climax dominant of the semi-arid western plains, is four times more abundant in the Fringe than in the Main Belt. The greater amount at the west is partly due to less rainfall but since the difference in rainfall is small the greater amount of buffalograss may better be attributed to greater relative area of clay soils. However, even on clay soils of the Fringe buffalograss is not regarded as a climax dominant but rather as a characteristic dominant of the grazing disclimax. Even in the disclimax it is apparently limited to soils of considerable clay content. Hundreds of buffalograss plants have been excavated throughout the Main Belt on soils mapped as Windthorst fine sandy loam but excavation always showed that the area occupied by buffalograss coincided with an area from which the fine sandy loam topsoil had been eroded, thus exposing the clay subsoil. Southward and westward, buffalograss has been frequently found on sands. Other species that are rarely encountered on sands of the Main Belt, but common on intermingled areas of clay, include *Stipa leucotricha, Bouteloua curtipendula, Sporobolus asper* var. *hookeri,* and Texas grama *(Bouteloua rigidiseta)*. Why these and buffalograss are here virtually limited to clays is not known. Competition from other species better suited to sands does not appear to be an adequate explanation because the same relations prevail on almost bared areas

TABLE 2. Comparison of vegetation of the Main Belt and Fringe portions of the Western Cross Timbers showing principal species and relative coverage of each.

Species	Coverage	
	Main Belt	Western Fringe
	Percent	*Percent*
All annual forbs	21.9	15.6
Buchloe dactyloides	3.7	15.2
Hordeum pusillum	...	7.8
Quercus stellata and Q. marilandica	9.4	5.4
Stipa leucotricha	2.6	5.3
Festuca octoflora	1.9	5.1
Aristida spp. (perennial)	2.8	5.1
Bromus spp. (annual)	0.9	3.6
Aristida spp. (annual)	8.5	3.3
Bouteloua hirsuta	6.1	3.1
Bouteloua curtipendula	2.5	2.9
Perennial forbs except Ambrosia	1.6	2.5
Schedonnardus paniculatus	1.6	2.0
Paspalum ciliatifolium	6.2	1.9
Prosopis juliflora	...	1.8
Ambrosia psilostachya	2.9	1.7
Cynodon dactylon	3.1	1.6
Eragrostis spp. (perennial)	1.8	1.5
Chloris verticillata	1.2	1.4
Andropogon saccharoides	4.4	1.2
Andropogon scoparius	0.4	1.1
Sporobolus asper and var's	0.1	1.1
Rhus trilobata	0.6	1.1
Leptoloma cognatum	0.4	1.0
Opuntia spp. (flat-stemmed)	0.3	1.0
Smilax bonanox	5.3	0.9
Poa arachnifera	...	0.7
Carex spp. and Cyperus spp.	0.3	0.6
Bouteloua rigidiseta	...	0.6
Cenchrus pauciflorus	0.8	0.4
Opuntia leptocaulis	...	0.3
Panicum scribnerianum	0.7	0.3
Bouteloua gracilis	...	0.3
Triodia pilosa	0.6	0.3
Bumelia lanuginosa	0.3	0.1
Forestiera spp.	0.8	...
Rhus copallina	0.7	...
Crataegus spp.	0.5	...
Andropogon ternarius	0.5	...
Other woody species*	2.2	1.0
Other grasses and grasslike plants*	2.4	1.2

*Species individually having less than 0.3 percent coverage in either western or eastern portions.

Studies of mineral nutrient requirements of the five species mentioned might disclose the reasons for their virtual absence on surface sands of the Main Belt.

From Table 2 it may be noted that certain species, whose principal range is in humid eastern United States, such as post oak and blackjack oak, fringeleaf paspalum *(Paspalum ciliatifolium)*, Bermudagrass *(Cynodon dactylon)*, and saw greenbrier *(Smilax bonanox)* have about twice as much or more coverage in the Main Belt as in the more arid Fringe. Certain other species such as hairy grama *(Bouteloua hirsuta)*, western ragweed *(Ambrosia psilostachya)*, and silver bluestem *(Andropogon saccharoides)*, which are generally associated with semi-arid climates, here attained their greatest relative coverage in the area of greatest available moisture. This may indicate the essentially mesophytic character of these species. Accordingly, in more arid climates one should expect to find them confined to sites of better than average moisture relations unless grazing or other disturbance had removed their normal competitors.

It is of interest to note that while hairy grama is most abundant in the Main Belt, the very closely allied blue grama *(Bouteloua gracilis)* is of importance only in the Fringe, thus indicating less exacting moisture requirements for the latter. Mueller and Weaver (1942) in testing drought resistance of seedlings found those of blue grama to be more resistant than those of hairy grama.

FLORISTICS BASED ON PHYSIOGNOMY AND SOILS

Several major vegetal types or plant communities are readily distinguished by general aspect alone. When the plots from the cross-country transects were segregated according to aspect-types, it was found that this also generally segregated plots on certain broad groups of soils. These are: (a) the post oak-blackjack oak-greenbrier type of Podzolic soils with gentle relief; (b) the post oak-blackjack oak-mesquite type of immature Reddish Prairie soils with rough relief; (c) the mesquite type of mature Reddish Prairie soils with gentle relief; (d) the old-field type of eroded Podzolic soils with gentle relief, characteristically treeless and dominated by annual species of *Aristida;* (e) the open prairie type of mature Reddish Prairie soils with gentle relief; and (f) the open prairie type, commonly including some live oak *(Quercus virginiana)*, of Rendzina soils with moderate relief.

The open prairie type of mature Reddish Prairie soils, (e) above, is quite uncommon and simply represents the original condition of the mesquite type prior to overgrazing and invasion by mesquite. The open prairie type of Rendzina soils, (f) above, may usually be identified by scattered live oak trees and outcroppings of limestone. Its total area within the Cross Timbers as mapped (Fig. 1) is small and the vegetation is very similar to that of the Fort Worth Prairie or northern Grand Prairie described by Dyksterhuis (1946). The first four types are the major physiognomic as well as edaphic units of the Western Cross Timbers. For brevity they may be referred to as: (a) the Quercus-Smilax type; (b) the Quercus-Prosopis type; (c) the Prosopis type; and (d) the old-field type. The relative coverage by the principal species within each is given in Table 3.

QUERCUS-SMILAX TYPE

The Quercus-Smilax type is characterized by the greatest abundance of oak and greenbrier both of which are universally present within the type. The type occurs on sandy Red and Yellow Podzolic soils of gentle or rolling relief (Fig. 11).

From Table 3 it may be noted that post oak and blackjack oak compose 25.8 percent of understory vegetation. The need for distinction between the Quercus-Smilax and the Quercus-Prosopis types also is apparent. In the latter the oaks constitute only 11.7 percent of coverage, while Smilax is five times more abundant in the Quercus-Smilax type than in

FIG. 11. The *Quercus-Smilax* type which characterizes podzolic soils of the Main Belt. The liana is saw greenbrier *(Smilax bonanox)*. The tree sprouts at the left are postoak and those at the right are blackjack oak. The understory shows dominant climax grasses, principally *Andropogon scoparius*, and commonly associated herbaceous perennials. *(Photo. by L. E. Reid, Jr.)*

the Quercus-Prosopis type. Annual forbs constitute a fifth of the vegetation but are abundant also in other types. The most common perennial grass of the Quercus-Smilax type is fringeleaf paspalum *(Paspalum ciliatifolium)* which was at least twice as abundant there as in other types. Other important perennial grasses in order of abundance were *Bouteloua curtipendula* or sideoats grama, *Stipa leucotricha* or Texas stipa, *Chloris verticillata* or tumble windmillgrass, *Eragrostis* spp. or perennial lovegrasses, and *Bouteloua hirsuta* or hairy grama. The first two were largely confined to areas where the clay subsoil of the fine sandy loam soils was exposed by erosion. From Table 3 it may be noted that a few species were imporatnt only in this type. Included were *Crataegus* spp. or hawthorns, *Triodia flava* or purpletop, *Rhus glabra* or smooth sumac, *Symphoricarpos orbiculatus* or coral-berry, and *Manisuris cylindrica* or jointtail.

QUERCUS-PROSOPIS TYPE

The Quercus-Prosopis type of immature Reddish Prairie soils occupies the areas of greatest relief. A type characterized by common mesquite of the arid southwest, and post and blackjack oaks of the humid north and east, approaches the mythical "Cattails and Cactus type" insofar as strange associates are concerned. The mesquite evidently has invaded in historical times but now grows intermingled and in competition with post oak and blackjack oak. The mesquite attains good size for the species while the oaks are near the margin of their range and scrubby (Fig. 12).

From Table 3 it may be noted that the oaks composed a tenth of understory vegetation while mesquite composed less than 1 percent coverage. However, mesquite has a very diffuse crown and is generally distributed so that this small amount is sufficient to lend definite character to the landscape.

TABLE 3. Major physiognomic as well as edaphic units or types of the Western Cross Timbers and relative coverage by the principal species within each.

SPECIES OR GROUPS	COVERAGE			
	Quercus-Smilax Type	Quercus-Prosopis Type	Prosopis Type	Old-field Type
	Percent	*Percent*	*Percent*	*Percent*
Quercus stellata and Quercus marilandica	25.8	11.7	—	0.4
Annual forbs	19.5	19.8	12.0	18.2
Smilax bonanox	10.4	2.0	—	3.7
Paspalum ciliatifolium	6.4	2.7	1.1	3.1
Bouteloua curtipendula	3.7	2.1	3.9	0.3
Stipa leucotricha	3.6	3.2	8.3	—
Chloris verticillata	3.0	0.6	1.1	2.0
Eragrostis spp. (perennial)	2.9	2.1	0.9	2.1
Bouteloua hirsuta	2.7	2.8	3.8	0.8
Festuca octoflora	2.4	4.9	4.3	5.8
Aristida spp. (annual)	2.3	1.2	0.4	37.0
Buchloe dactyloides	2.3	12.0	20.6	0.4
Schedonnardus paniculatus	1.9	0.6	3.9	0.5
Panicum scribnerianum	1.8	0.4	0.2	0.2
Bromus spp. (annual)	1.6	4.6	1.4	0.2
Perennial forbs except Ambrosia	1.6	1.6	3.7	2.0
Carex spp.	1.2	1.4	—	—
Andropogon scoparius	1.2	1.4	1.1	0.2
Ambrosia psilostachya	1.1	1.2	1.6	6.8
Aristida spp. (perennial)	1.1	6.6	4.3	1.7
Andropogon saccharoides	0.9	0.6	1.9	2.8
Cynodon dactylon	0.4	2.7	—	3.7
Bumelia lanuginosa	0.4	0.2	—	—
Crataegus spp.	0.4	—	—	—
Cornus asperifolia	0.2	0.2	—	—
Cenchrus pauciflorus	0.2	—	—	2.5
Triodia flava	0.2	—	—	—
Rhus glabra	0.2	—	—	—
Symphoricarpos orbiculatus	0.2	—	—	—
Manisuris cylindrica	0.2	—	—	—
Hordeum pusillum	—	4.3	14.1	3.1
Rhus trilobata	—	2.4	—	—
Elymus canadensis	—	1.1	—	—
Sporobolus asper	—	1.1	0.9	—
Leptoloma cognatum	—	0.6	1.7	1.1
Bouteloua rigidiseta	—	0.5	0.8	—
Ulmus crassifolia	—	0.5	0.2	—
Poa arachnifera	—	0.5	—	—
Prosopis juliflora	—	0.5	3.4	—
Bouteloua gracilis	—	0.3	0.4	—
Triodia pilosa	—	0.3	0.2	—
Opuntia spp. (flat-stemmed)	—	0.3	2.0	—
Celtis spp.	—	0.2	—	—
Muhlenbergia reverchoni	—	0.2	—	—
Agropyron smithi	—	0.2	—	—
Opuntia leptocaulis	—	—	0.5	—
Sporobolus cyrptandrus	—	—	0.5	—
Panicum obtusum	—	—	0.3	—
Condalia obtusifolia	—	—	0.2	—
Andropogon ternarius	—	—	—	0.6
All others*	0.2	0.4	0.3	0.8

*Species individually having less than 0.2 percent coverage.

Buffalograss was the most abundant perennial grass. Others in order of abundance were perennial threeawns (*Aristida* spp.), Texas stipa, hairy grama, and fringeleaf paspalum. Perennial species of threeawn were more abundant in this type than in the others as were also annual brome grasses. Skunkbush sumac *(Rhus trilobata)*, Canada wildrye *(Elymus canadensis)*, Texas bluegrass *(Poa arachnifera)*, hackberry (*Celtis* sp.), seep muhly *(Muhlenbergia reverchoni)*, and bluestem wheatgrass *(Agropyron smithi)* were

FIG. 12. The *Quercus-Prosopis* type which characterizes the immature Reddish Prairie soils of rough relief of the Fringe. Crowns of post oaks in left background are partly hidden by the lighter colored foliage of a mesquite tree *(Prosopis juliflora)*. On the right is a blackjack oak showing size at maturity at this location. The understory is composed principally of annuals and cacti which, with mesquite, characterize degeneration of original vegetation under overgrazing.

abundant only in this type. The bluegrass, wildrye, and wheatgrass were largely limited to colluvial or alluvial soils within the type.

PROSOPIS TYPE

The Prosopis type is characterized by an overstory of common mesquite on mature Reddish Prairie soils of gentle or flat relief. This type represents the "included prairies" of earlier authors. They are small inclusions of the extensive bodies of Reddish Prairie soils that occur to the west and north of the Cross Timbers proper. They were originally treeless but are now, almost without exception, invaded by mesquite (Fig. 13).

From Table 3 it may be noted that the Prosopis type is virtually devoid of trees except common mesquite. Two shrubby plants are important only in this type. They are tasajillo *(Opuntia leptocaulis)* and lotewood condalia *(Condalia obtusifolia)*. Buffalograss composed a fifth of the vegetation and was almost twice as abundant as in the Quercus-Prosopis type. Annual forbs were roughly half as abundant as in the other three types but the annual grass, little barley *(Hordeum pusillum)*, was three times more abundant than in any other type. In addition to buffalograss, other important perennial grasses in order of abundance were Texas stipa, perennial species of Aristida, sideoats grama, tumblegrass *(Schedonnardus paniculatus)*, and hairy grama. Vine-mesquite *(Panicum obtusum)* was important only in this type.

OLD-FIELD TYPE

This type consists of formerly cultivated land, cleared, cultivated, and abandoned because of erosion. It is almost wholly within the area of Podzolic soils of gentle to rolling relief (Fig. 14).

From Table 3 it may be noted that annual species of threeawn (*Aristida* spp.) compose more than a third of the vegetation and other annual grasses a tenth. An additional fifth is composed of annual forbs. While the perennial, western ragweed *(Ambrosia psilostachya)* composes almost 7 percent of the total. Splitbeard bluestem *(Andropogon ternarius)* is important only in this type.

CLIMAX OR ORIGINAL VEGETATION

Vegetation evidently present at the time of settlement, on mature soils, and still present locally where it has escaped major disturbance, is usually climax or original vegetation. A sample of a relict plant community which the evidence indicates to be a fair representation of the original vegetation of the Main Belt of the Cross Timbers is illustrated at two seasons in Figures 15 and 16.

FIG. 13. The *Prosopis*-type of mature Reddish Prairie soils of "flats" within the Fringe. Such included prairies were open grassland at the time of settlement, but are now either cultivated or invaded by mesquite. Cattle are shown grazing winter annuals and the cool-season perennial, *Stipa leucotricha*, in mid-April. Such disclimax plant cover occasionally provides good winter and spring pasturage though production is less certain and of smaller amount than potential for the site as shown in Figure 3.

In the case of the Western Cross Timbers the term "original vegetation" is not strictly synonymous with "climax vegetation" since the overstory of oaks constitutes a postclimax (Weaver & Clements, 1938). The nature of the climax and use of relicts were described by Clements (1934, 1936).

Studies of the original vegetation are necessary for correct interpretation of current floristic composition in relation to past or potential composition. They provide an ecologist with bases for a dynamic classification of plant communities. A range ecologist must consider the original vegetation of a given site in order to judge potential species composition, forage production, and soil stability. On range lands the present vegetation is often not a satisfactory indicator of potential vegetation. The site and particularly the soil are usually far more reliable as indicators of potential plant cover than is present-day vegetation, provided, of course, that relicts of the original vegetation for the specific soil have been examined. Under climax or original conditions, close correlation no doubt existed between type of vegetation and type of site. Now, however, the vegetation of a range or pasture is partially a product of the grazing use it has received. It no longer reflects only the effect of climate on development of vegetation and soil. Type of soil and type of vegetation are temporarily not in equilibrium even though the unifying effect of climate will eventually reestablish such an equilibrium if disturbance is removed. Under grazing, the soil deteriorates much more slowly than the vegetation. Meanwhile the soil profile retains characteristics that enable ecologists to associate it with other areas of essentially the same soil on which climax or undisturbed vegetation is still present as a guide to potential floristic composition and forage production. The foregoing concept has been applied in the present studies. After the major soil differences of the area had been classified, several areas of relict vegetation were located on each. Samples of two tracts of undisturbed original vegetation for each of the three major edaphic conditions are given in Table 4.

From Table 4 it will be noted that little bluestem (*Andropogon scoparius*) was clearly the major climax dominant over wide differences in soils, as well as at widely separated locations throughout the area. It appears safe to conclude that little bluestem originally constituted two-thirds of the understory vegetation of uplands in the Western Cross Timbers. Samples of relicts of the Fort Worth Prairie on the east by Dyksterhuis (1946) showed essentially this same percentage of little bluestem. The Fort Worth Prairie is treeless. It receives slightly more rainfall but, since the soils are clays rather than sands, infiltration and available water are less. Also, the greater

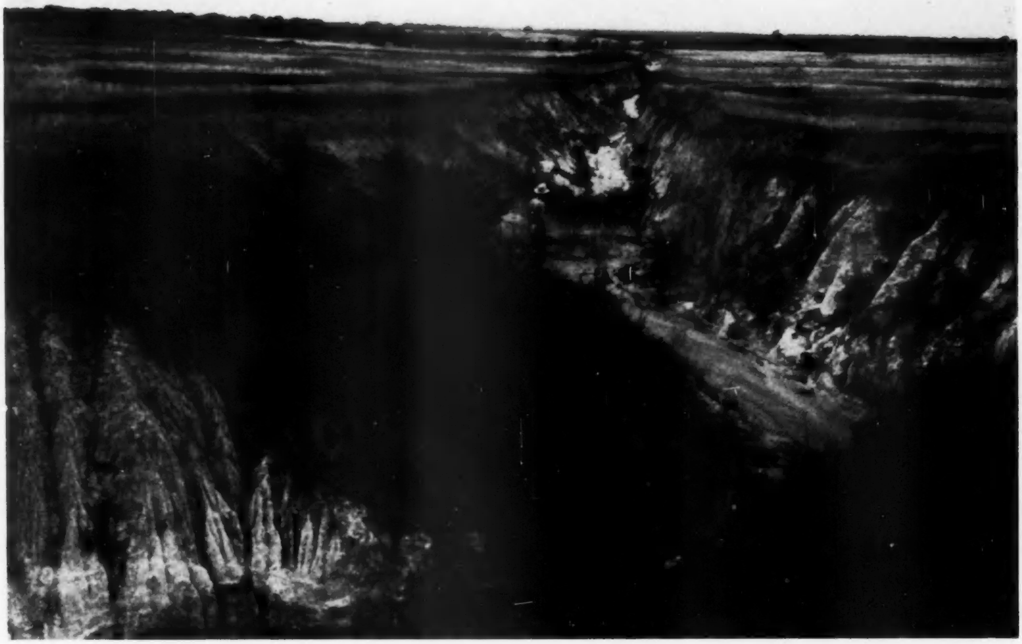


FIG. 14. The old-field type of cleared, cultivated, eroded, and abandoned fields occurs primarily on Red and Yellow Podzolic soils of gentle relief. Blocks of the original oak cover are shown in the background. The plant cover on the old fields is principally annual threeawns (*Aristida* spp.).

relief permits greater run-off. The data in Table 4 show the highest percentages of little bluestem on mature Reddish Prairie soils even though this area receives the least precipitation and is generally composed of clay soils. This might be considered an anomaly were it not for the almost level relief that strongly favors infiltration of rainfall and the absence of competition from oaks for the available water.

Table 4 shows that the two climax tall grasses, big bluestem (*Andropogon furcatus*) and Indiangrass (*Sorghastrum nutans*), were generally distributed and important. Among the mid grasses little bluestem, sideoats grama, and tall dropseed (*Sporobolus asper* and varieties) were found at all the stations. Hairy grama (*Bouteloua hirsuta*) was the only short grass which occurred widely in relict vegetation. Significantly, buffalograss was absent. The coverage percentages of the dominant grasses mentioned tend to emphasize uniformity of the original vegetation of the Western Cross Timbers despite wide differences in soils. Comparison of Table 4 with Table 3 will show that differences between the vegetation of the various soils are greater now than they were originally. It may be concluded that different soils once supported essentially the same flora but that they differ greatly in their ability to sustain such comparable original vegetation under the same degree of grazing disturbance.

Despite more homogeneity in climax vegetation than in disclimax vegetation, some significant variations in the original vegetation were found associated with different soils. Podzolic soils were characterized by general occurrence of Scribner panicum (*Panicum scribnerianum*), sand lovegrass (*Eragrostis trichodes*), and purple lovegrass (*E. spectabilis*). One species, *Sporobolus macrus*, was found only on Podzolic soils. Numerous species that were important constituents of relict vegetation on both Podzolic soils and immature Reddish Prairie soils were virtually absent from relicts on mature Reddish Prairie soils. These included smallsnout sedge (*Carex microrhyncha* Mack.), *Panicum scribnerianum*, *Quercus stellata*, *Quercus marilandica*, and native perennial species of lespedeza. Certain species were important only on mature Reddish Prairie soils. These included *Carex microdonta* Torr. et Hook., and heath aster (*Aster ericoides*).

COMPARISON WITH AVERAGE DISCLIMAX

The average coverage by important species in all samples of relict vegetation may provide an indication

FIG. 15. A relict of the original vegetation of the Main Belt of the Western Cross Timbers, showing growth in mid-April after being burned in January. The scale, in feet, shows height of a pure stand of *Sorghastrum nutans*. The understory is principally *Andropogon scoparius*. Mature post oaks are shown in the foreground with an all-aged stand in the background. The earliest accounts of the Cross Timbers presumably describe the type of savannah shown.

FIG. 16. A relict of the original vegetation of the Main Belt, showing one year's growth of the climax grasses. *(Photo. by B. W. Allred.)*

of the composition of the original vegetation over the whole area. The similarity in coverage of important species on various soils in widely separated locations was noted in Table 4. An average of all samples of original vegetation is compared with average present-day vegetation in Table 5.

Table 5 indicates that the two tall grasses, *Sorghastrum nutans* or Indiangrass, and *Andropogon furcatus* or big bluestem, have been almost wholly displaced since occupation of the area by settlers. The mid grass *Andropogon scoparius* has been reduced from its position as a major dominant to a minor constituent of the vegetation. The short grass *Bouteloua hirsuta* has increased. *Buchloe dactyloides*, another short grass, is most abundant among perennial grass invaders. Annuals of many kinds are now the principal feature of the vegetation though almost nonexistent in the original vegetation. Not less than eleven perennial species, virtually absent in the original vegetation, now compose recognizable percentages of the composition. An almost complete change in composition of vegetation is indicated. In general, the change is characterized by displacement of mid and tall grasses by short grasses and by displacement of long-lived perennials by annuals and short-lived perennials. Some species nonpalatable to livestock have invaded.

GRAZING COACTIONS IN MAIN BELT

Two types of ecologic interactions have been defined by Weaver and Clements (1938) and Clements and Shelford (1939). They define "coaction" as the influence of two or more species or individuals upon each other, whereas "reaction" is defined as "the collective effect of organisms upon the habitat." The degeneration of Cross Timbers vegetation already de-

TABLE 4. Samples from two tracts of relict original vegetation for each of the three major edaphic conditions of the Western Cross Timbers showing relative coverage by the principal species within each.

PRINCIPAL SPECIES	Podzolic soils; fine sandy loams: gentle relief		Immature Reddish Prairie soils: rough relief		Mature Reddish Prairie soils; clays: flat relief	
	Cundiff*	Nocona	Alvord	Post-oak	Bowie	Jacksboro
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Andropogon scoparius	62	68	47	70	70	72
Sorghastrum nutans	7	8	2	5	8	4
Andropogon furcatus	3	—	P**	P	1	16
Eragrostis trichodes	3	P	—	—	—	—
Sporobolus macrus	2	—	—	—	—	—
Bouteloua curtipendula	1	1	11	P	2	1
Sporobolus asper and var's	1	P	8	P	1	3
Carex microrhyncha	1	2	2	P	—	—
Panicum scribnerianum	1	1	P	P	—	—
Eragrostis spectabilis	1	P	—	—	—	—
Poa arachnifera	1	P	P	1	—	—
Muhlenbergia reverchoni	—	—	—	—	—	2
Carex microdonta	—	—	—	—	P	1
Bouteloua hirsuta	—	3	5	12	1	P
Manisuris cylindrica	—	1	—	—	1	—
Panicum virgatum	—	—	—	—	3	—
Panicum linearifolium	—	—	4	—	—	—
Bouteloua gracilis	—	—	—	6	—	—
Quercus stellata	3	7	8	1	—	—
Quercus marilandica	P	1	2	P	—	—
Other woody species	1	1	4	P	—	—
Psoralea tenuiflora	4	1	P	—	—	—
Lespedeza spp. (perennial)	1	3	3	P	—	—
Artemisia spp. (herbaceous)	1	P	P	—	—	—
Tephrosia virginiana	—	P	1	—	—	—
Aster ericoides	—	—	—	—	4	P
All others	7	3	3	5	9	1

*Name of town nearest to relict.
**"P" indicates that the species was present on the tract but composed less than 0.51 percent of the sample of coverage.

scribed is a result of many such complex interactions.

In grazing coactions the primary relation is food supply. Climax prairie vegetation evolved under grazing by native animals and such a coaction may be considered normal. Grazing by domestic livestock, within fenced pastures, often with no guide to proper season or proper numbers except current profits, may be expected to result in abnormal coactions. Abnormal coactions soon become evident by changes in the species composition of the vegetation. No less real are the resultant changes in the diets of the grazing animals as one kind of plant is displaced by another, often with a different season of growth. Hart, Guilbert, and Goss (1932) found remarkable changes in the nutritive content of range plants related to stage of growth and degree of bleaching and leaching of dead material. Moreover, they found differences between species and their relative abundance more important nutritionally than difference in locality where the species grew.

Changes in relative abundance of species, of Podzolic soils of the Main Belt of the Cross Timbers, that have resulted from unmanaged grazing by domestic livestock are illustrated by comparison of Tables 3 and 4. It may be noted that little bluestem, with

TABLE 5. Change in composition of the vegetation of the Western Cross Timbers, since settlement, as reflected in relative coverage by the principal species of a composite sample of original vegetation, contrasted with a composite sample of present vegetation.

PRINCIPAL SPECIES	Original vegetation	Present vegetation
	Percent	*Percent*
Andropogon scoparius	64.8	0.8
Sorghastrum nutans	5.7	—*
Andropogon furcatus	3.3	—
Bouteloua hirsuta	3.5	4.6
Bouteloua curtipendula	2.7	2.7
Sporobolus asper and var's	2.2	0.6
Quercus spp.	3.7	7.4
Annual forbs	—*	18.8
Annual grasses (except Aristida)	—	10.2
Buchloe dactyloides	—	9.4
Aristida spp. (annual)	—	5.9
Aristida spp. (perennial)	—	4.0
Paspalum ciliatifolium	—	4.0
Stipa leucotricha	—	4.0
Andropogon saccharoides	—	2.8
Cynodon dactylon	—	2.4
Ambrosia psilostachya	—	2.3
Schedonnardus paniculatus	—	1.8
Chloris verticillata	—	1.3
Prosopis juliflora	—	0.9
Percent of total coverage	85.9	83.9

*Bars denote coverages of less than 0.51 percent.

an original coverage of about 65 percent, now has coverage of only about 1 per cent. Post oak and blackjack oak, which once comprised only about 5 percent of total understory vegetation, now comprise about 26 percent. Indiangrass, which originally had about 7 or 8 percent coverage, now has less than 0.2 percent. Annual forbs, which were practically absent from areas of relict vegetation, now comprise about 20 percent of total coverage. Many species, which were practically absent in tracts of relict original vegetation, are important constituents of the grazing disclimax. Included are *Paspalum ciliatifolium, Stipa leucotricha, Chloris verticillata, Festuca octoflora*, annual species of Aristida, *Buchloe dactyloides, Schedonnardus paniculatus*, annual species of Bromus, *Ambrosia psilostachya*, and *Andropogon saccharoides*. Some naturalized exotic species, such as *Cynodon dactylon*, persist locally in the disclimax. Other naturalized exotics, such as *Sorghum halepense*, persist for but a few years under intensive grazing. Certain species of the climax as indicated by Table 4 have apparently increased in relative coverage under grazing. These include *Bouteloua curtipendula, Panicum scribnerianum*, and the woody species as a group. Other species of the original vegetation of the Main Belt are virtually absent in the grazing disclimax. Among these are *Andropogon furcatus, Eragrostis trichodes, Sporobolus macrus*, and *Poa arachnifera*.

SPECIES CHOSEN BY RANGE CATTLE EACH MONTH

Causes for specific changes in species composition that occur on range land may well be sought by study

of the grazing habits of livestock. That range livestock select certain species is generally appreciated, but the extent to which selection by one class of livestock is affected by time of year and rate of stocking has received little attention. Yet the application of such knowledge to possible adjustments of numbers and seasons of use in order to favor increase of certain forage species, or to hasten secondary succession on range land, is clear.

The annual cycle of daily weather events long has been faithfully recorded and is appreciated by laymen as having a profound influence on both plants and animals. Strangely, seasonal changes in the grazing habits of range livestock on any one range are largely unknown to range operators, nor is there much literature dealing specifically with the subject. A notable exception is the pioneering work of Cory (1927) who provided a comprehensive record of the daily activities of cattle, sheep, and goats on range land of the Edwards Plateau of Texas. His data included a table of percentages of total forage supplied by different plant species and groups of species in the year-round grazing activities of the three kinds of animals. This was followed (Fraps & Cory, 1940) by a report of the percentages of different kinds of vegetation consumed by each kind of animal through 15 months which then served as the basis for determining chemical composition of forage consumed by animals grazing the same range year-round. How greatly the level of nutrition might have been influenced by a lower rate of stocking and hence greater opportunity for the animals to select different species in different seasons remains unknown. Also unknown is the relation between the range vegetation of the study and range vegetation which would occupy the same area under range regeneration or degeneration. The grazing habits of cattle on tame pastures in relation to forage available per unit of area and to management practices have been reported by Johnstone-Wallace and Kennedy (1944). There are many reports dealing with choice of certain cultivated species in certain seasons by domestic livestock but few indeed reporting species that compose the diet of range livestock on an annual basis. No doubt this is true because we ordinarily do not observe both vegetation and grazing animals closely at the same location systematically through the year. Livestock men of the Cross Timbers were asked if cattle grazed the oaks more during certain months than other months, if they were grazed at all except under duress, and if so, when? To such questioning there were only the vaguest of replies. Yet oak shoots were found to constitute at least one-half of the bulk of the diet of Cross Timbers cattle in parts of April and were taken by choice only in April. Samples of the parts of post oak and blackjack oak chosen by cattle were obtained for chemical analyses. In April the new stems with their leaves broke off readily at the point of junction with the previous year's wood, and the cattle ate the entire succulent shoot. The new stems had not yet developed woody tissues, were 1 to 4 inches long, and thickly crowded with immature leaves. The chemical analyses made by the Texas Agricultural Experiment Station showed that both post oak and blackjack oak had over 16 percent protein, and over 0.70 percent phosphoric acid; a diet comparing favorably with the best and supercharged with constituents deficient in winter.

The importance of the relation between stage of plant growth and ability to withstand grazing is well known. Much has been learned recently about the intimate relation between stage of growth and nutritive value of the forage for livestock. Fudge and Fraps (1945) found range grasses of the Western Cross Timbers to be generally deficient in protein and phosphoric acid after June. Much remains to be learned about seasonal differences in chemical composition as related to seasonal differences in species chosen by livestock.

The preference for different plants or species of plants by livestock under range conditions appears to vary from month to month in a manner strikingly similar to changes in relative protein and phosphorus contents among available forage species or individual plants. Thus, livestock grazing in a pasture having a mixture of species will select different species at different times of the year and these have commonly proved to be the species which were most beneficial for the livestock at that time of the year. This should not lead to the assumption, however, that livestock regularly select plants on the basis of protein or mineral content. Livestock avoid certain species in all seasons of growth evidently because of odor or flavor. Furthermore, thorough research with palatable species showed correlation of palatability with only two variables, and they were water content and carotene (Archibald, Bennett, & Ritchie, 1943). Water content, protein, and phosphorus are commonly highest in young green shoots and decrease in successive stages of plant development. The importance, from a nutritional standpoint, of knowing annual developmental history is apparent.

Monthly visits to the same pastures have shown that prominent forbs are largely either nonpalatable throughout the year or are unpalatable by the time they become prominent. In the monthly surveys this meant that cattle were observed selecting some particular forb difficult to identify because the species had not yet produced flowers. Usually the forb would be in the stage where it was a leafy shoot three to eight inches tall. Upon revisiting the area one month later, plants of that species which had escaped grazing could usually be positively identified. The forb would then be in flower, its lower leaves fallen, and the whole carefully avoided by livestock whose preference had meanwhile shifted to another forb. The latter would meanwhile have grown from some obscure ground-layer plant of the previous month to a species of considerable coverage with leafy stems 3 to 8 inches tall. Thus, grazing preceded blossoming, and loss of palatability, through a long series of forbs with different seasons of growth. Upon blossoming, each species was usually ignored so completely by livestock that one might conclude it never had been

grazed. For numerous kinds of annual forbs the date of blossoming signalled loss of palatability for the remainder of the year.

One fact which cannot be overemphasized is that green succulent forage, rich in protein and phosphorus, is so scarce during winter that range livestock keep winter rosettes of most forbs closely cropped and seek out all grasses showing any trace of greenness. They commonly grazed off much old growth on otherwise unpalatable species in their eagerness to reach short green winter shoots at the bases of species which at first appeared dormant. Close observation has indicated that native species vary considerably, not only in period of dormancy, but also in winter-hardiness of the foliage produced by non-dormant species. Species selected at any one date are likely to be the species most succulent at that date unless they are wholly nonpalatable year-round. The species selected by livestock on a given range vary not only with season but also with intensity of grazing, or rate of stocking. It will be understood that livestock can exhibit little choice on a closely grazed range. Thus the herd of cattle, being observed monthly on a closely grazed range, selected several species in the drought of July and August that the herds on moderately and lightly stocked ranges did not graze in that period. Close grazing over long periods alters floristic composition which in turn affects relative palatability.

Data on species chosen by cattle each month through one year on a lightly to moderately stocked range of typical vegetation and soils of the Main Belt of the Western Cross Timbers are shown diagrammatically in Figure 17.

Figure 17 shows that on lightly to moderately stocked ranges of ordinary present-day vegetation, some 60 species may successively compose an important part of the diet of range cattle through the course of the year. It is evident from the data that a species cannot well be called nonpalatable without first having made observations throughout a full year. Furthermore, terms commonly applied to native forage plants such as unpalatable, very palatable, moderately palatable, etc., should properly be qualified by stating not only the time of year, but also the intensity of grazing. Some very common species of the Cross Timbers that are not listed in Figure 17 were, nonetheless, chosen seasonally on overstocked ranges. For example, on such ranges the annual snakeweed or "broomweed" *(Gutierrezia dracunculoides)* was heavily grazed in July. Furthermore, though post oak and blackjack oak were grazed on all ranges in April they were grazed again in July and August only on greatly depleted and heavily overstocked ranges. Only a few species appeared to be wholly nonpalatable at all seasons, even where livestock were virtually starving. Widespread species in this category were Baldwin ironweed *(Vernonia baldwini)*, green antelopehorn *(Asclepiodora viridis)*, prairie dogbane *(Apocynum sibiricum)*, and buffalobur nightshade *(Solanum rostratum)*.

Apart from consideration of periods during which individual species were chosen, the monthly observations and year to year observations have led to the following general conclusions: The bulk of the diet of range cattle of the Main Belt consists of forage from woody species in April, forbs in May, and grasses in June. Native legumes constitute a major part of the diet only in July. Winter rosettes are an important part of the diet from December through March. Beginning each year near the middle of February there is a transition period during which the bulk of material grazed by range livestock changes from old and dry to new and green foliage. On overgrazed ranges this transition is not completed until mid-April when new oak leaves become sufficiently abundant to carry the entire grazing load. The numerous winter annuals associated with overgrazed range provide scarcely any winter forage on the sandy uplands of the Cross Timbers. On moderately stocked ranges in good condition, this transition to fresh forage may be almost complete by March 1 rather than by mid-April. Three reasons for this difference are: (1) Ranges in good condition have more of the earlier perennial species such as Texas bluegrass, Canada wildrye, and early perennial forbs; (2) ranges in good condition have large, dense bunches of grass (particularly bluestems) from which green leaves emerge earlier than from closely cropped bunches; and (3) such ranges do not have all fresh growth grazed off immediately after it appears—hence, accelerated growth is possible in late winter.

AUTECOLOGY OF PRINCIPAL GRASSES

Autecology is commonly defined as the ecology of individuals (Weaver & Clements 1938). It is only natural that the preceding study of plant communities (synecology) should focus attention upon certain species because of local or general abundance, either in climax or disclimax vegetation. In applied range ecology the season of use, kind and class of grazing animals, and numbers to be grazed are necessarily considered in the light of their effect upon the predominant species in any one pasture or natural area. It is obviously not possible to graze each species to a desired degree in mixed native vegetation. The autecology of individual species is of paramount importance because season, kind, and intensity of grazing must be suited to maintenance or increase of certain species. This is accomplished only through intimate knowledge of such key species, particularly their local seasonal development, since livestock select different species from month to month, largely on the basis of relative succulence.

The following accounts of behavior of individual species refer only to development of ungrazed plants in the Main Belt. References to choices by cattle refer to choices under light stocking rates in ordinary mixed vegetation of the Main Belt unless otherwise noted. The yields of six of these grasses on the adjoining Fort Worth Prairie have been reported in pounds per acre by months (Dyksterhuis 1946).

Andropogon scoparius, or little bluestem, has been shown to be the principal climax dominant of the

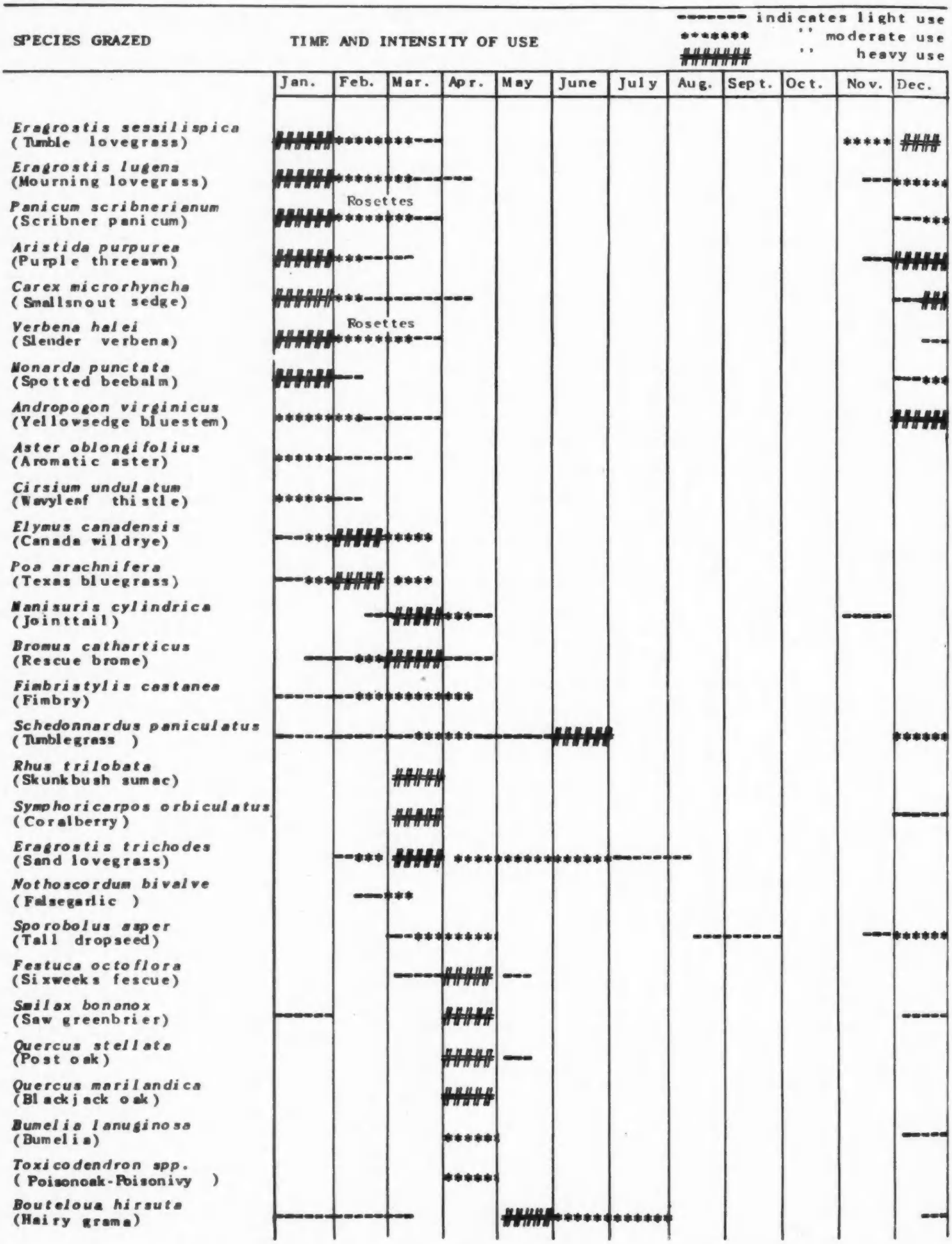
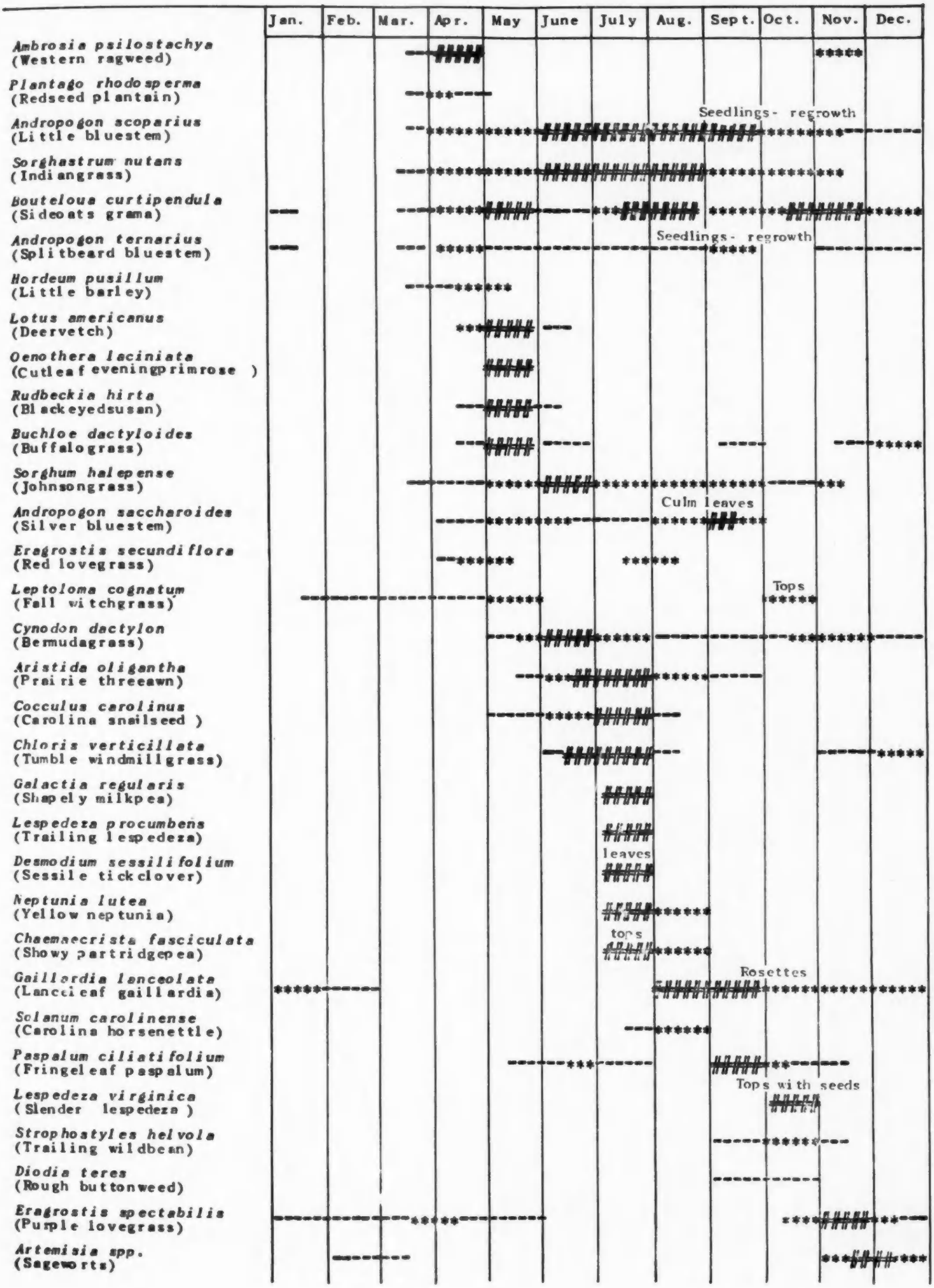


FIG. 17. Chart showing species which composed an important part of the diet of range cattle through 12 months in the Main Belt. The range was lightly to moderately stocked and consisted of both uncleared lands and old fields. Months in which a species was chosen are shown to the nearest one-half month, and the degree to which the species was grazed during this period is indicated by symbols for light, moderate, and heavy use. The chart is continued on the next page.

FIG. 17. (Continued)



Western Cross Timbers. This warm-season midgrass composed two-thirds of the total vegetation of all relict areas sampled and is found throughout. It is plainly the key species in the management of all ranges except those to be reserved for winter grazing where a cool season grass might be favored. It had less than 1 percent coverage in the average of all samples of disclimax vegetation. The reasons for this response to unmanaged grazing are traceable to its upright habit and long season of palatability which on year-round range enables livestock to remove virtually all of its food-manufacturing surface. The species was not observed to go completely dormant at any season but most nearly approached it in January. Even then, the larger bunches had some bluish-green new shoots around the edges and in the interior where they were protected by old foliage. In February, the tallest new leaves were 3 inches long; by March they were 6 inches long; in April, 12 inches; in May, 24 inches; and in June, 30 inches long. In June, natural seedlings of the current year are commonly 3 to 4 inches tall. In July, flowering culms could be found within the sheaths of most plants and the earliest culms were partly exserted. Also, in July the oldest foliage of the current year turned reddish at the tips. During August there was further dying back of foliage from the tips, and numerous blades and sheaths died to the base. The plants as a whole, however, retained a bluish-green to gray appearance which might be mistaken for drought dormancy if viewed from a distance. During August the growth of the flowering culms appeared to be at a standstill. In September the flowering culms were fully exserted but spikelets were still generally contracted and appressed along the racemes. In October the opening of spikelets was general, thus exposing numerous hairs and making the hairy racemes prominent from some distance. Also in October, numerous new tiller shoots originated at the bases of the plants while the spring foliage turned red. During November the racemes disarticulated and flowering culms turned red. The narrow new autumnal blades at the base of the plant attained a length of about 6 inches. During December the blades, sheaths, and culms produced in spring and summer all acquired the characteristic reddish color associated with climax True Prairie in winter. However, at this latitude dormancy is more apparent than real because autumnal shoots originated at the base more or less continuously from October into December and portions remained green through the winter. The longest of autumnal shoots were also reddish at the tips, particularly where unprotected by old growth. On ranges with great diversity of species from which to choose, livestock take little bluestem by choice from mid-March into November. It provides the most nutritive and most palatable forage in March, April, May, and June. It is considered as relatively good forage in July and August because it is not nearly as severely affected by the usual summer drought which forces less deeply rooted species into virtual drought dormancy. It is fair grazing in September, October, and November but makes fibrous and poor forage in January and February. On lightly stocked ranges cattle obtain some green forage from this species in every month of the year. Under such conditions the plants are grazed from the side rather than from above because the new leaves extend from the sides of the central column of dried shoots. Cattle apparently find little difficulty in wrapping their tongues about these green leaves and excluding any dried and fibrous parts. It is of interest that material gathered in this way pulls out from the base of the central column, breaking at the tender meristematic region near the ground line rather than breaking off at the animal's jaws. Thus portions of the blades and sheaths highest in moisture, protein, and phosphorus content are gathered into the animal's mouth. This is in marked contrast to many other forage species. It will be clear that analyses of protein and phosphorus from clippings made parallel with the ground do not reflect the true nutritive value of this species when grazed, rather than when fed as hay. The disparity between real value and value as shown by chemical analyses increases as the season advances because cattle become more selective with respect to portions of each plant selected after the pasturage as a whole becomes less succulent. One has only to observe cattle grazing what may appear to be dry and stemmy little bluestem in July and August to understand the shortcomings of ordinary clipped samples as a means of determining either the nutritive value of the forage or the effect of this season of grazing on the welfare of the plants. One quickly observes that no dry stems are ingested. Instead the white ends of green blades and sheaths pulled from the dense interior of the bunch constitute a large part of the material ingested. In September, on lightly grazed ranges of little bluestem, the coaction takes another important turn. During this month cattle were commonly observed to spend a large part of the time feeding exclusively upon the exserted immature inflorescences (Fig. 18). The effect on nutrition of cattle should be expected to be entirely different than analyses of the whole plant might indicate. The effect of the animals on the plants is commonly such that virtually the entire seed crop is consumed. Since the fruits are immature at this time, it may be assumed that they are digested. Natural reseeding is thus delayed another year, whereas one month of protection at the time of maturation of seeds might have insured an abundant source of seed. Cornelius (1947) showed that ecotypes in the United States vary greatly in seasonal development and forage production.

Sorghastrum nutans, or yellow Indiangrass, is the second most important climax dominant. It composed almost one-tenth of the vegetation of relict areas and was an important constituent of all relicts of climax vegetation. In the Western Cross Timbers this warm-season rhizomatous tall grass has behaved as a decreaser under grazing. In the grazing disclimax, its coverage was less than 0.5 percent. The species most nearly approached dormancy in January but rhizomes could be found with the tips of new

FIG. 18. Plant of little bluestem *(Andropogon scoparius)* showing loss of the seed crop for the year because cattle grazed the immature inflorescences. Scattered plants of little bluestem on improving range are commonly "topped" by cattle in this manner year after year. Dominance by little bluestem and excellent range condition, is correspondingly delayed.

green leaves extending from their ends. Such new leaves were exserted a centimeter or more between frosts but were repeatedly killed back to the ground line by frosts. The old foliage retained a reddish color. In February old leaves were faded to light orange and old sheaths and culms were discolored to a dirty gray. The short, new leaves continued to be exserted from the ends of the rhizomes and younger rhizomes were elongated horizontally. In March new rhizomes pointed upward abruptly and numerous green leaves were exserted to a height of 3 inches. In April the tallest leaves were 12 inches long. In May they were 20 inches long, and in June they were 24 inches long. Also in June, numerous new rhizomes broke the surface and broad blades appeared at the tops of the plants. By July the leaves were 30 inches long, by August broad blades near the tops of the plants had turned an orange color and basal foliage of the current year was about 34 inches long. In September flowering culms were found in the sheaths. Also, numerous green shoots to 6 inches long arose near the bases of the plants while the older foliage attained a length of 40 inches. In October flowering culms were exserted, closely followed by anthesis (Fig. 19). The 6-inch basal leaves of the previous month attained a length of 12 inches while the spring foliage turned an orange color. In November inflorescences shattered, the flowering culms turned straw-colored, blades and sheaths of spring origin turned reddish or orange, and the blades of September origin, now 2 feet in length, began to dry at their tips. In December, the plants were dormant except for the bases of the shoots of September origin. Natural seedlings emerged in the following March and April. This species was equal to little bluestem in palatability but greatly exceeded it in amount of forage produced per unit of area. Its rhizomatous habit permits greater food storage and partial independence of seed production as a means of propagation. These features may provide some advantages over little bluestem under close grazing. When both are grazed as closely as they can be cropped by livestock, the normally taller stature of this species means in effect that a higher percentage of its food-manufacturing surface is removed in grazing. However, its rhizomatous habit may account for the fact that Indiangrass did not decrease as greatly nor as rapidly as little bluestem when both received the same degree of grazing disturbance.

Bouteloua hirsuta, or hairy grama, had a coverage of 3.5 percent in areas of relict vegetation. In such areas it was normally limited to the most arid sites and it is probably to be regarded as a component of the original vegetation of preclimax sites rather than as a climax dominant. Under grazing use it increases and spreads to soils of ordinary depths. It was

FIG. 19. Yellow Indiangrass *(Sorghastrum nutans)* is a rhizomatous warm season tall grass that ranked second to little bluestem among the climax grasses.

found to compose 4.6 percent of the disclimax vegetation. It was almost twice as abundant in the Main Belt of the Cross Timbers as it was in the Fringe. The species was grazed less than little bluestem or Indiangrass. Its inherently low stature provides an additional advantage in competition with taller species where all are closely grazed. It is an increaser throughout the grazing disclimax. It was grazed in January and February and again from May to July. It did not go dormant through January and February but rather showed numerous green internodes. New foliage appeared in March and continued to grow through June. In July the plant approached drought dormancy but in August the first inflorescences appeared. In September the inflorescences were bluish but turned gray in October when seeds began to shatter and the foliage shriveled. During November and December the internodes were bright green but there were very few green blades. Some unusual specimens on loose sand were observed to have reclining culms with roots at the nodes.

Bouteloua curtipendula, or sideoats grama, had a coverage of 2.7 percent in relicts of climax vegetation. The data indicate exactly the same percentage of coverage in the present vegetation. Many pastures, however, showed the species to be an increaser in the grazing disclimax. This warm season, rhizomatous mid-grass is capable, under grazing, of carrying a high percentage of its foliage within a few inches of the ground. Its low stature under these conditions and its vigorous rhizomatous habit are believed to be responsible for its persistence and even increase under severe grazing disturbance. As previously noted, however, initial increase is followed by decrease as degeneration of the forage cover continues. Sideoats grama was virtually dormant in January when old foliage weathered to a dirty pinkish color with old flat blades recurved so that the blunted tips rested on the surface. In February some plants had shoots green at the base but with tips killed by frost and turned yellow while old foliage had weathered to a dirty gray. By March new green shoots were three inches long. Rapid growth occurred in April. In May the new foliage was 10 inches long. In June there was prolific production of inflorescences. In July and August the numerous inflorescences matured and shattered seeds while new inflorescences continued to appear and the tips of the earliest foliage dried. September brought a marked increase in production of inflorescences or "a second crop." In October there was prolific production of new shoots from the bases of the plants. In November the spring foliage dried to the ground while autumnal shoots continued green. In December the plant approached dormancy with most of the foliage turning a light pink color. In mixed vegetation, cattle kept sideoats grama closely grazed from May through August and again from October to November. It was grazed the least in February.

Sporobolus asper, or tall dropseed, and its varieties are treated collectively in the quantitative data. The group had 2.2 percent coverage in relicts of climax vegetation and 0.6 percent coverage in the grazing disclimax. A more intimate knowledge of this polymorphic species has been attained since the quantitative field data were obtained. The species and its two varieties are more readily distinguished ecologically than taxonomically. No doubt the varieties should have been separated in the original survey. *Sporobolus asper*, or tall dropseed, is the least abundant and occurs primarily in areas protected from overstocking. In the Cross Timbers it occurs almost exclusively on sands. It makes small tufts from which coarse stiff flowering culms arise. *Sporobolus asper* var. *pilosus*, or hairy tall dropseed, though a midgrass, is easily the smallest plant of the three. Its sheaths are somewhat hairy and the foliage commonly is bluish when growing. The culms are slender. It is the most palatable and occurs characteristically on the shallower soils within the range of the group. It, too, is apparently a decreaser on ordinary upland and seldom occurs on lowland. *Sporobolus asper* var. *hookeri*, or meadow tall dropseed, makes large clumps of extremely long tapered leaves. It is largely limited to lowlands and deep-clay uplands receiving run-in water. In contrast to the other two members of the group, this variety is plainly an increaser in the grazing disclimax. Of the three tall dropseeds mentioned, the variety *pilosus* is most abundant in the Fringe while the species is most abundant in the Main Belt. Another perennial *Sporobolus* is of particular interest because the original collection of this species within Texas was made in two different areas of relict Cross Timbers vegetation. This is *Sporobolus macrus*, or Mississippi dropseed, a rhizomatous warm season mid-grass.

Buchloe dactyloides, or buffalograss, though virtually absent in relicts of climax vegetation, is, nonetheless, the principal dominant of the grazing disclimax. Its invasion or increase under grazing is largely due to its low growth-form which enables it to escape excessive removal of its food-manufacturing surface. Under intensive stocking it escapes rather than tolerates heavy grazing. This warm season stoloniferous short grass had a coverage of 15.2 percent in the western Fringe of the Cross Timbers, but only 3.7 percent in the Main Belt. Even this small percentage in the Main Belt was not generally distributed but occurred upon areas of exposed clay subsoil where the normal layer of fine sandy loam topsoil had been eroded away. The species exhibited no real dormancy, though new growth was repeatedly killed by frosts throughout January and February. It very nearly approached drought dormancy during July and August but commonly resumed active growth in September and October. It dried rapidly in November and December.

The perennial species of Aristida or threeawns constitute an important group of generally weedy bunch grasses of low palatability that increase under intensive grazing. Together they composed 4 percent of the disclimax vegetation. Their coverage in the western Fringe was almost twice as great as in the Main Belt. *Aristida purpurea* or purple three-

awn is believed to be the most common perennial threeawn but other closely related species of the Group Purpureae are readily confounded in extensive surveys of grazed vegetation. Also, surveys may or may not be made at the optimum time for identification of threeawns. Only one perennial threeawn was obviously different from the others with respect to response to grazing. This was *Aristida purpurascens* or arrowfeather threeawn. It was usually the only perennial threeawn in relict vegetation. Furthermore, it was absent in adjoining grazed areas where the Group Purpureae was most abundant. Arrowfeather threeawn is plainly a minor climax mid grass that decreases with grazing disturbance whereas species of the Group Purpureae increase or invade. It is of interest that species of this group behaved as cool season perennials, making their maximum vegetative growth during the cool part of the year and flowering most abundantly in spring. In contrast, arrowfeather threeawn went dormant in the winter, broke dormancy in March, and flowered in summer and fall like other warm season perennials. The Group Purpureae was grazed by choice from December to March, whereas arrowfeather threeawn is grazed by choice from March to December.

Paspalum ciliatifolium or fringeleaf paspalum is a dominant of disclimax vegetation though absent in relicts of climax vegetation. It was the principal perennial grass of the Main Belt with 6.2 percent coverage. It composed only 2 percent of the vegetation in the Fringe. It was an important element of the composition of formerly cultivated fields where it had an average coverage of about 3 per cent. Most specimens remained dormant through January, February, and March. Though green shoots a few millimeters in length may appear at the bases of some young leaves in March, these are killed back to the ground even by light frosts. During the period from January to March, the old leaves weathered from clear brown color to a dirty deep brown and finally disintegrated almost completely. In April new shoots reached a length of 4 inches. In May these attained a length of 7 inches and the earliest inflorescences were exserted from the sheaths with culms reaching a length of 12 inches. In June leafy shoots reached a length of 12 inches. Meanwhile, the naked slender culms of the inflorescences elongated surprisingly, thus moving the inflorescences and fruits over and through surrounding vegetation to a horizontal distance of 2 to 3 feet or more from the parent plant. In July the first crop of fruits was disseminated while the culms and broad upper leaves turned brown. In August and September new shoots arose from the base reaching a foot in length. In October the second crop of inflorescences was produced which again disseminated seed at considerable distance from the parent through extraordinary elongation of the procumbent culms. This elongation of flowering culms was not observed where the plants were grazed repeatedly. In November dissemination of seed was completed and the broad blades at the base of the plant died gradually from the tip back. In December the naked culms became straw-colored and leaves and sheaths were brown, excepting the newest portions of the plants which remained green. In mixed vegetation the species was grazed by choice primarily in September when plants of this species attained maximum development. It composed a large part of the diet of livestock in September in most Cross Timbers pastures. It was taken only sparingly in other months of the growing season and not at all in winter. The species was plainly dependent on marked disturbance and was therefore classified as an invader.

Stipa leucotricha, or Texas stipa, ranked fifth among perennial grasses of the Western Cross Timbers disclimax with a coverage of 4 percent. It was only half as abundant in the Main Belt as in the Fringe. On some areas of clay soils it was the principal grass. In the Main Belt it was found to be largely limited to exposed clay subsoils. It was practically absent in relicts of climax vegetation. This cool season mid-grass increased or invaded under grazing on all soils excepting coarse sands where it appeared unable to ecize. Many features of its autecology in this same general climate have been reported by Dyksterhuis (1945, 1946). It was demonstrated that this bunch grass may propagate itself by means of basal cleistogenes even where grazing is sufficiently intense to prevent development of flowering culms.

Andropogon saccharoides, or silver bluestem, is a warm-season mid grass dominant of the grazing disclimax. It had a coverage of 2.8 percent over the broad area but was almost four times as abundant in the Main Belt as in the Fringe. It was virtually absent in relicts of climax vegetation. The species remained dormant through January, February, and March. During this period the woody culms remained erect but there was a gradual loss of blades, with sheaths weathering from reddish to gray, while the culms remained bright straw-colored. In April new leaves originated at the ground line, and also at the nodes of old culms to a height of 1 foot above the ground. Some shoots attained a length of 6 inches in April. In May new shoots were 14 inches tall and there was much tillering at the base. The first crop of inflorescences was produced almost simultaneously. In June new foliage attained a height of 16 inches and flowering culms a height of 30 inches. In July and August the hairy spikelets were carried to great distances by the wind, leaving the long exserted culms and the white-hairy racemes. During the same period new and broader, shorter leaves developed at a height of a foot from the ground on the old flowering culms, while many of the earlier lower leaves disintegrated. In September a second crop of inflorescences was produced along with a new crop of tiller shoots near the bases of the old plants. Again new broad leaves were produced at a height of 2 feet from the surface and 6 to 12 inches below the new inflorescences, the latter being borne on naked culms. In October and November the second crop of racemes disarticulated and all foliage turned a deep red as the species entered dormancy in

November. Grazing animals appeared to select the plant primarily in September when the new broad blades about 2 feet from the surface were grazed. However, basal leaves were relished in April and May but at that time other equally or more palatable foliage was abundant. On heavily stocked ranges where normal development of the plant is prevented, it may be continuously cropped from April to July and again from September to November. Under intensive grazing it becomes virtually drought dormant in July. The early and late crops of inflorescences have caused a common misconception that this species provides grazing both exceptionally early and also late in the grazing year. In reality, this species is among the last to resume growth in the spring and is one of the first to go dormant in the fall. This characteristic, along with its habit of regularly producing two crops per year of seed which are readily carried by the wind, and its suffruticose habit, may account for its increase under overgrazing and its early entrance on abandoned fields.

Cynodon dactylon, or Bermudagrass, is an introduced, rhizomatous and stoloniferous, warm-season, short grass. It composed 3.1 percent of the vegetation of the Main Belt but was only half as abundant in the Fringe. Where naturalized on uplands it produced little forage though it made a rather complete cover in local colonies a few feet across. It was not observed to make extensive stands on upland unless cultivated or fertilized, and mowed or closely grazed to prevent growth of taller species. Where naturalized on native range it was dormant in January and February. In March new leaves were exserted from within sheaths of the previous year; not always from below the soil surface. Inflorescences appeared in July and again in November. Growth virtually ceased during the normal summer drought but growth in the fall continued after warm-season native species such as big bluestem had gone dormant. The last green shoots were killed by frost and these weathered from yellow to gray as winter advanced.

Panicum scribnerianum, or Scribner panicum, is a species that is almost universally present in the Western Cross Timbers in both climax and disclimax situations. It apparently increases slightly for a time as climax vegetation degenerates under grazing after which it, too, may decrease. Its seasonal development is of special interest because of the unusual though intimate relation between its stages of development and grazing coactions. Cattle choose this plant on much the same basis that spinach and lettuce and other rosette species are chosen by humans. Only the rosette stage is grazed, the rosette leaves being eagerly sought throughout the period that they are available. When the plant bolts the rosette stage in spring, cattle discontinue grazing it until the following fall when new rosette leaves are again developed. In January the dried summer leaves two inches long were grouped at the tips of naked culms and old foliage was a yellowish tan. At the bases of old culms were bright green rosette leaves, 1.5 inches long, and twice as broad as the summer leaves. Some horizontal shoots of the rosette were 2.5 inches long. In February the dried upper leaves were weathered to a dirty tan, while rosette blades and shoots measured about the same length as in January, though the shoots were more numerous. In March the old summer leaves had weathered to gray and plants were beginning to bolt the rosette stage with new shoots extending vertically to a height of six inches and with blades 2.5 inches long. In April the new shoots were 8 inches tall. The lower blades were drying, the earliest inflorescences could be found in the upper sheaths, and cattle no longer grazed the plant. In May the leafy shoots were 12 inches tall with inflorescences exserted an additional 12 inches on naked culms. The plants were in full anthesis and no evidence remained of the earlier winter rosettes. Also, the culm leaves of the previous summer had disintegrated. In June seeds were shed while the flowering culms turned straw-colored and many of the longer leaves were lost. In July and August many new, shorter, narrower blades were produced in dense bunches at the tops of culms, while older, lower leaves were lost. The long naked flowering culms produced in May broke off level with the upper tufts of leaves, leaving little trace of their presence earlier in the year. In September and October a second crop of inflorescences was produced but these were among the upper leaves, whereas the crop of May was exserted on long naked culms. The crop of September and October was only partly exserted from the sheaths. During the same period winter rosettes began to develop. In November the second crop of seeds was shed, the shoots and leaves produced in summer dried, and winter rosettes attained full winter width but not density. In this month livestock resumed grazing the species. In December the narrow brush-like aggregates of summer leaves near the tops of the plants turned orange color while the rosettes remained bright green.

The presence of several perennial species of Eragrostis in the Western Cross Timbers, and their virtual absence on the adjoining Fort Worth Prairie, provided one of the greatest contrasts between the two plant communities. Five species composed about 2 percent of the vegetation of the Western Cross Timbers. They are generally distributed but are most abundant in the Main Belt. They are *Eragrostis lugens* or mourning lovegrass, *E. sessilispica* or tumble lovegrass, *E. secundiflora* or red lovegrass, *E. spectabilis* or purple lovegrass, and *E. trichodes* or sand lovegrass. The five species vary greatly in their responses to disturbance and in their seasonal development. The first three cannot withstand the competition of the climax plant community whereas *E. spectabilis* and *E. trichodes* are minor climax dominants. *Eragrostis lugens* and *E. sessilispica* are cool season grasses whereas the remaining three are warm season grasses. *Eragrostis lugens*, *E. secundiflora* and *E. sessilispica* are most common on formerly cultivated, sandy fields. *E. lugens* is occasionally found on dense clays of the adjoining overgrazed prairies. *E. trichodes* is virtually limited to sandy areas pro-

tected from grazing while *E. spectabilis* occurs in both climax and disclimax situations.

Andropogon ternarius, or splitbeard bluestem, composed a very small percentage of the total vegetation of the Cross Timbers but on many formerly cultivated fields it composed half or more of the total vegetation in the next to the last stage of the subsere. When inflorescences are not present, it is sometimes confounded with little bluestem, though the species is of lower stature, has narrower leaves, and differs in other ways. Inflorescences readily distinguish it because of the pairs of white-hairy racemes, or the so-called split beard. In January the dried foliage was reddish and the old culms remained erect, each tipped with a ring of hairs. In February and March old flowering culms usually broke near the ground line, whereas those of little bluestem remained erect. In April the new foliage attained a length of 6 inches. In May there was complete exsertion of the first crop of inflorescences while the foliage attained a length of ten inches. In June the racemes disintegrated while foliage attained a length of 16 inches. In July and August the last of the inflorescences disintegrated and the entire plant took on a reddish cast. In September the second crop of inflorecsenses could be found in the sheaths and some new tiller leaves were produced. In October a second and more abundant crop of inflorescenses than the May crop was produced. In November and December there was rapid disintegration of racemes and drying of the entire plant to a reddish color. In mixed vegetation it was grazed by choice in April and September. It was relished least in February and March.

RANGE DEGENERATION OR CONDITION CLASSES

Changes in the vegetation of the Western Cross Timbers have been described in terms of averages in preceding sections. However, average vegtation probably does not exist on individual ranges. Rather one encounters various degrees of range degeneration ranging from almost climax cover to almost bare soil or dense woods.

The process of degeneration under unlimited grazing has characteristics which are probably universal. These have been succinctly stated by Weaver and Clements (1938) as follows: "The more palatable species are eaten down, thus rendering the uneaten ones more conspicuous. This quickly throws the advantage in competion to the side of the latter. Because of more water and light, their growth is greatly increased. They are enabled to store more food in their propagative organs as well as to produce more seed. The grazed species are correspondingly handicapped in all these respects by the increase of less palatable species and the grasses are further weakened by trampling as stock wanders about in search of food. Soon bare spots appear that are colonized by weeds or weedlike species. The weeds reproduce vigorously and sooner or later come to occupy most of the space between the fragments of the original vegetation. Before this condition is reached, usually the stock are forced to eat the less palatable species, and these begin to yield to the competition of annuals. If grazing is sufficiently severe, these, too, may disappear unless they are woody, wholly unpalatable, or protected by spines." It may perhaps be added that among mixed grasses of nearly equal palatability, the tallest and most productive species lose the highest percentage of their photosynthesizing surface when all are grazed as closely as possible. Hence, under continued unmanaged grazing, palatable species of tall grasses are replaced by mid grasses and these are in turn replaced by short grasses with corresponding reductions in annual production of forage.

In applied range ecology the entire course of degeneration is commonly divided into four "range condition classes" called excellent, good, fair, and poor range condition. Range condition for a specific site may be expressed quantitatively as the percentage of current total coverage by vegetation which is normal (or edaphically climax) vegetation for that site. In practical applications the possible range in values from zero to 100 percent may well be divided into four equal parts, described qualitatively. Thus, range with between 75 and 100 percent coverage by original vegetation would be termed in excellent condition, and so on through the four classes. Typical plant communities that occur in the Main Belt of the Western Cross Timbers were selected to represent ranges in excellent, good, fair, and poor condition. The four range conditions or degrees or degeneration are illustrated in Figs. 20, 21, 22, and 23, respectively.

Figures 20 through 23 show characteristic alterations in overstory vegetation that accompanied range deterioration. Large quantities of dried plant materials once contributed to hot ground fires that killed the lower branches on the oaks as illustrated in Figs. 15 and 16. With intensive grazing and absence of fuels for hot fires the density of the stand of oaks increased, but, also, the number of lower branches increased as a range deteriorated from excellent to good condition. As range deteriorated from fair to poor condition, grazing became sufficiently intense to reduce numbers of lower branches and produce a browse-line as shown in Fig. 23. This was, of course, accompanied by virtual destruction of the normal understory of perennial grasses.

The composition of the vegetation of the four typical range conditions, illustrated in Figs. 20, 21, 22, and 23, is given in Table 6.

Data on a few key species or groups are often adequate to determine range condition after the process of deterioration for a specific site is known. This is exemplified by selecting the key species and groups from the data given in Table 6. It may be noted that at the four points in degeneration, or range condition classes, little bluestem composed 68, 32, 15, and less than 1 percent respectively, of total coverage. Corresponding amounts of annuals were 1, 4, 14, and 46 percent, respectively. Corresponding amounts of trees and shrubs were 10, 14, 16, and 36 percent, respectively. Little bluestem decreased, annuals invaded, and woody plants increased. The

FIG. 20. Range in excellent condition on Windthorst fine sandy loam soil. A veteran post oak is shown in left background. The trees may have a few more low branches than occurred in the original savannah (Fig. 15) but the climax grasses still extend to their boles. *(Photo. by Mack McConnell.)*

relative coverage by these key species or groups clearly indicates range condition.

Smith (1940) classified range plants according to behavior under grazing. He recognized species that decreased, species that increased, species that invaded, and species more or less unaffected. Weaver and Hansen (1941) have shown that in degeneration of grassland under grazing, species may be classified in one of three categories. They are: (1) Species of the climax that simply decrease, here named Decreasers; (2) species of the climax which increase in relative abundance, at least for a time, after which they too may decrease, here named Increasers; and (3) species that are not present in climax communities but enter or invade disturbed areas, here named Invaders. The data in Table 6 shows little bluestem in the role of a decreaser, woody vegetation as an increaser, and annuals as invaders.

On improving range the same three categories of species are discernible by the fact that species of the first group increase, species of the second group increase for a time, after which they decrease toward percentages found in climax vegetation, and species of the third group are eliminated (Dyksterhuis 1946).

Degeneration of vegetation on immature Reddish Prairie soils of the Fringe of the Western Cross Timbers is similar in some respects to that of the Main Belt, but was not studied intensively. It differs in many respects. There is a great increase of the short grasses before annuals become predominant. Common mesquite has invaded most stands of the oaks. Comparison of Tables 3 and 4 shows that whereas mesquite is absent on relict vegetation of immature Reddish Prairie soils, it has 0.5 percent coverage in the grazing disclimax. Due to the open character of the crown this 0.5 percent represents considerable crown area. Flat-stemmed opuntias, though absent on relicts, were conspicuous in the disclimax. *Rhus trilobata* had increased generally except on goat ranges where it was commonly absent. The oaks, which increased greatly under grazing in the Main Belt, showed little or only local evidence of having done so in the Fringe.

SUBSERES ON FORMERLY CULTIVATED FIELDS OF MAIN BELT

Subseres, or courses of secondary succession, on abandoned croplands have received the attention of numerous ecologists. Studies with certain applications here include those of Smith (1940) in central Oklahoma who reported both floristic and faunal

FIG. 21. Range in good condition on Windthorst fine sandy loam. The density of the stand of oaks has increased, part of the understory is occupied by minor climax grasses that have increased and other plants have invaded. Little bluestem has decreased. In the absence of fire and destructive grazing the crowns of the oaks, particularly blackjack oak, extend to the ground and climax grasses are largely forced to their perimeters.

changes though the latter were found of minor importance; of Booth (1941) in east-central Oklahoma and southeastern Kansas whose findings were most closely paralleled by those to be reported; of Drew (1942) in Missouri who also provided a most helpful review of literature on the subject; and of Warner (1945) in southeastern Iowa who provided detailed analyses of effects of different covers on plant growth conditions resident in soils.

Formerly cultivated fields are a characteristic feature of the landscape in the Main Belt. Such old fields are readily recognized in all stages of secondary succession by angular perimeters, by virtual absence of oaks, and by presence of numerous gullies. The annual threeawn stage of the subsere, shown in Figure 14, was the most common and covered the greatest area. However, subseres on different fields exhibited every stage of secondary succession.

The time required to complete a subsere on any one field was found to vary greatly depending upon: (a) the adequacy of the source of seed of successionally higher species; (b) the degree of grazing disturbance; and (c) the degree of erosion at the time of abandonment. The nature of the subsere, as well as the time required, may be somewhat altered by any one of the above factors.

SUBSERE PROTECTED FROM GRAZING

The subsere on abandoned fields protected from grazing was studied first. These fields had a fair source of wind-borne seed of climax species within one-quarter mile or less of their boundaries. All old fields studied were on Windthorst fine sandy loam, cleared, cultivated, and abandoned because of erosion.

The first stage was always composed of common weeds of cropland that were present under cultivation. During the first year of abandonment, forbs were most prominent and attained large size due to wide spacing. In the second year their robust stems remained standing amongst dwarfed successors (Fig. 24). Coverage by species in Figure 24 was approximately as follows: six-weeks fescue *(Festuca octoflora)*, 18 percent; prairie threeawn *(Aristida oligantha)*, 15 percent; pepperweeds (*Lepidium* spp.), 12 percent; camphorweed *(Heterotheca subaxillaris)*, 10 percent; horseweed fleabane *(Erigeron canadensis)*, 8 percent; rough buttonweed *(Diodia teres)*, 7 percent; cutleaf evening primrose *(Oenothera laciniata)*, 5 percent; Johnsongrass *(Sorghum halepense)*, 5 percent; annual plantains (*Plantago* spp.), 5 percent; western ragweed *(Ambrosia psilostachya)*, 2 percent; Carolina geranium *(Geranium carolinianum)*, 2 per cent; and all others, 11 percent.

Even during the first year, the subsere species that would dominate the second stage were already present and began rapid aggregation about the parent plants. As pointed out by Clements (1916), aggregation tends to produce dominance while migration to great distances has an opposite effect. Aggregation leading

FIG. 22. Range in fair condition on Windthorst fine sandy loam soil. The oaks show some evidence of grazing by a faint browse-line and by sprouts near the bases of trees. The understory vegetation has been greatly altered and climax grasses that decrease are found primarily in clumps of sprouts where they receive some protection from grazing.

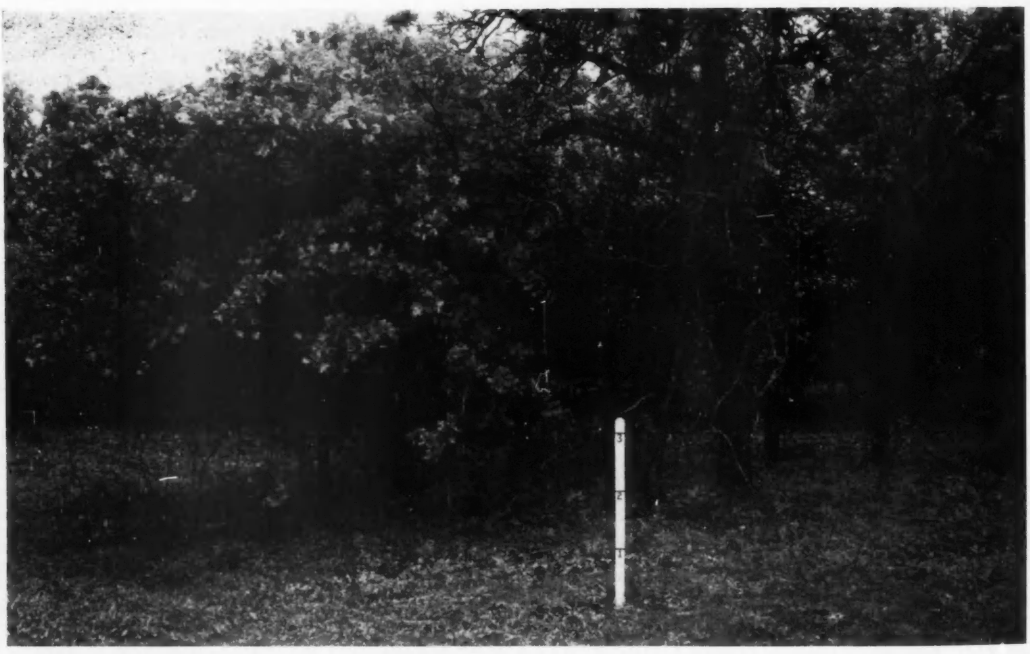


FIG. 23. Range in poor condition on Windthorst fine sandy loam soil. The crowns of the oaks make almost a continuous canopy below which is a distinct browse-line. The understory consists primarily of low growing annuals, weakly perennials, nonpalatable forbs, and the fallen leaves of the oaks.

FIG. 24. First or forb stage of the subsere of old fields. The area is in its second growing season after abandonment. Corn stalks are still evident on the surface. Stems of widely spaced, robust forbs that occupied the area the first year are still standing. Closely spaced plants of the second growing season are shown as they appeared in mid-April.

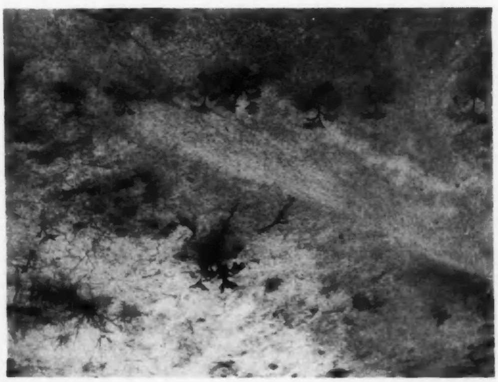


FIG. 25. Pioneers of exposed subsoil showing development in mid-April. The pen lies in a family of prairie threeawn *(Aristida oligantha)*. The thriving seedlings are aggregated along the prostrate culms of the single dead parent of this annual that became established in the preceding year. This threeawn dominates the second stage of the subsere. Linear migration of western ragweed *(Ambrosia psilostachya)* is shown in the foreground. The row of 10 new plants all arose from a single horizontal rootstock beneath the surface. This type of migration is one reason for early and continued prominence of western ragweed on old fields. The darkest colored plant at center is Carolina horsenettle *(Solanum carolinense)*.

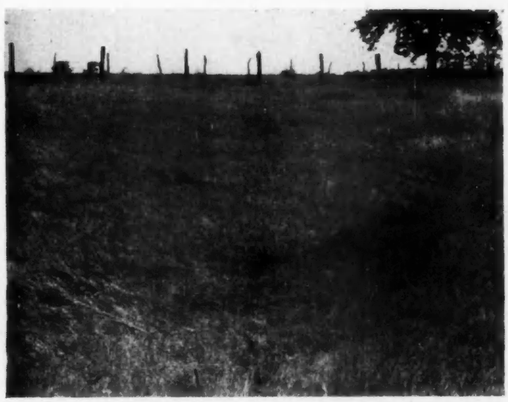


FIG. 26. Second or annual threeawn stage of the subsere of old fields. Scattered clumps of darker foliage in the mass of threeawn are silver bluestem *(Andropogon saccharoides)* whose feathery propagules are carried great distances by the wind.

to dominance of prairie threeawn and western ragweed in the second stage of the subsere is shown in Figure 25.

In the third year many common weeds of cropland were greatly dwarfed or eliminated while the annual threeawns and associates increased until by

TABLE 6. Changes in composition of vegetation resulting from overgrazing. Important species and their relative coverage are shown at four points in the course of degeneration of range land of the Western Cross Timbers. The four points are representative of ranges in excellent, good, fair, and poor condition on Windthorst fine sandy loam soil.

COMMON NAMES	SCIENTIFIC NAMES	RANGE CONDITIONS AND COVERAGE			
		Excellent	Good	Fair	Poor
		Percent	*Percent*	*Percent*	*Percent*
Little bluestem	Andropogon scoparius	68	32	15	—
Indiangrass	Sorghastrum nutans	8	4	—	—
Post oak	Quercus stellata	8	10	12	23
Perennial lespedezas	Lespedeza spp.	3	2	—	—
Hairy grama	Bouteloua hirsuta	3	—	5	—
Grasslike plants	Carex, Cyperus and Juncus	2	5	3	—
Sideoats grama	Bouteloua curtipendula	1	11	6	—
Jointtail	Manisuris cylindrica	1	—	—	—
Scribner panicum	Panicum scribnerianum	1	9	1	3
Tall dropseed	Sporobolus asper	—	7	5	—
Western ragweed	Ambrosia psilostachya	—	5	12	—
Blackjack oak	Quercus marilandica	—	3	3	6
Silver bluestem	Andropogon saccharoides	—	3	5	—
Tumble lovegrass	Eragrostis sessilispica	—	—	8	—
Splitbeard bluestem	Andropogon ternarius	—	—	3	—
Prairie threeawn	Aristida oligantha	—	—	3	10
Fall witchgrass	Leptoloma cognatum	—	—	2	—
Purpletop	Triodia flava	—	—	2	—
Blackeyedsusan	Rudbeckia hirta	—	—	2	4
Annual plantains	Plantago spp.	—	—	2	5
Baldwin ironweed	Vernonia baldwini	—	—	2	1
Fringeleaf paspalum	Paspalum ciliatifolium	—	—	1	4
Mourning lovegrass	Eragrostis lugens	—	—	1	—
Sixweeks fescue	Festuca octoflora	—	—	1	6
Rough buttonweed	Diodia teres	—	—	—	8
Southwestern carrot	Daucus pusillus	—	—	—	5
Spotted beebalm	Monarda punctata	—	—	—	4
Saw greenbrier	Smilax bonanox	—	—	—	4
Violet woodsorrel oxalis	Oxalis violacea	—	—	—	3
Carolina geranium	Geranium carolinianum	—	—	—	3
Slender verbena	Verbena halei	—	—	—	2
Other forbs*		2	2	5	9
Other perennial grasses*		1	7	1	—
Other trees or shrubs*		2	—	—	—
TOTALS		100	100	100	100
Annuals		1	4	14	46
Herbaceous perennials		89	82	70	18
Trees and shrubs		10	14	16	36

*Included are all species with less than 1 percent coverage.

the third or fourth year the threeawn stage was dominant (Fig. 26).

Coverage by species in the threeawn stage illustrated in Figure 26 was approximately as follows: prairie threeawn, and Kearney threeawn *(Aristida intermedia)*, 79 percent; western ragweed, 4 percent; rough buttonweed, 3 percent; least daisy *(Chaetopappa asteroides)*, 2 percent; blackeyedsusan *(Rudbeckia hirta)*, 2 percent; annual plantains, 2 percent; and all others, 8 percent.

Scribner panicum *(Panicum scribnerianum)* and purple lovegrass *(Eragrostis spectabilis)* enter early

FIG. 27. Purple lovegrass *(Eragrostis spectabilis)* at left, and Scribner panicum *(Panicum scribnerianum)* at right showing appearance in mid-April. These two perennial grasses are shown established in the annual threeawn stage. They are also present in climax cover but attain greatest coverage before the final stage.

in the subsere and are also present in the climax stage. However, they attain greatest relative coverage before the climax stage. Both are characteristically present in the threeawn stage (Fig. 27).

The threeawn stage may pass directly into the little bluestem *(Andropogon scoparius)* stage if an adequate source of seed is present in the form of old plants in adjoining woods or fence rows. Such old plants establish scattered seedlings to a distance of about 100 yards from parent plants. The early successful migrants become foci of families that eliminate annual threeawn through competition (Fig. 28).

The annual threeawn stage was usually followed by the splitbeard bluestem *(Andropogon ternarius)* stage, evidently because an adequate source of little bluestem seed was lacking. Under such conditions the much more feathery propagules of splitbeard bluestem may be carried to the old field from considerable distances. After some plants are established, aggregation is rapid, and the splitbeard bluestem stage occupies the field (Fig. 29).

Coverage by species in the splitbeard bluestem stage, illustrated in Figure 29, was approximately as follows: splitbeard bluestem, 56 percent; western ragweed, 7 percent; fall witchgrass *(Leptoloma cognatum)*, 5 percent; silver bluestem *(Andropogon saccharoides)*, 4 percent; annual threeawn, 4 percent; showy partridgepea *(Chaemecrista fasiculata)*, 4 percent; purple lovegrass, 2 percent; slender lespedeza *(Lespedeza virginica)*, 2 percent; and all others, 16 percent.

Entrance of little bluestem into the splitbeard bluestem stage may be delayed many years. Evidently lack of seeds of little bluestem is the primary cause for persistence of the splitbeard bluestem stage because the former appears to ecize readily in a dense stand of the latter. Observation of the two species

FIG. 28. Little bluestem *(Andropogon scoparius)* invading an old field. A fully developed parent plant is shown in front of the scale (in feet). Aggregation of progeny to the leeward of the parent plant is shown in the foreground. The age of the parent is unknown. Its progeny in mid-April varied from minute seedlings to plants beginning their third year.

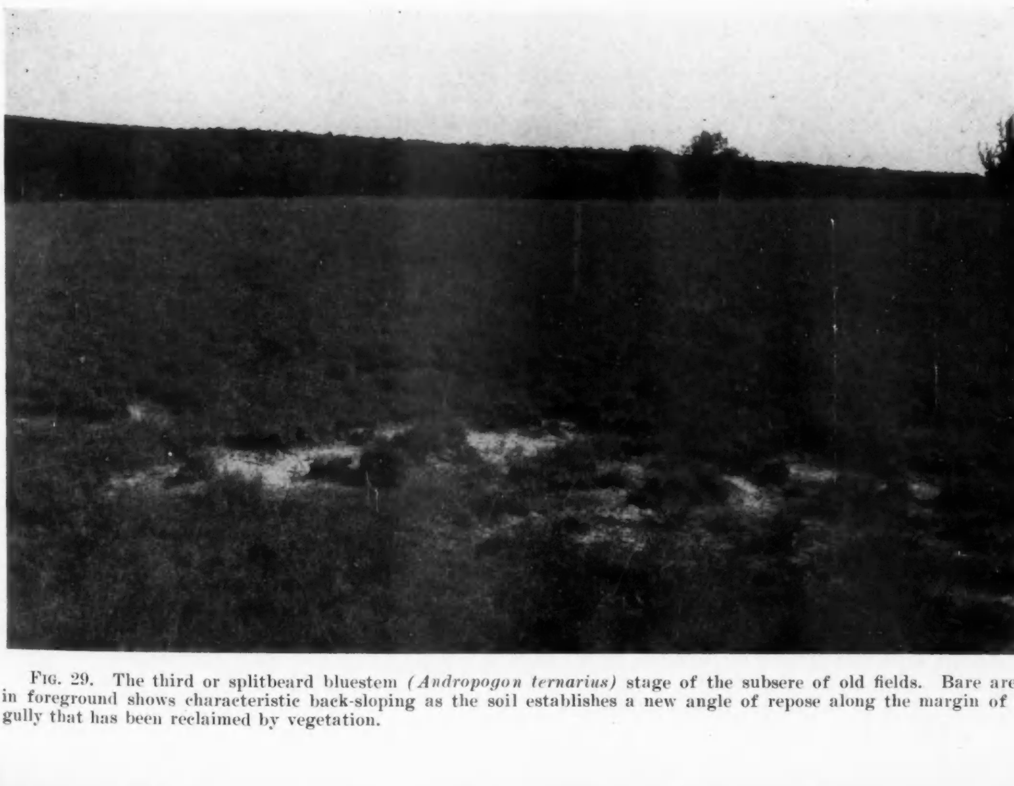


FIG. 29. The third or splitbeard bluestem *(Andropogon ternarius)* stage of the subsere of old fields. Bare area in foreground shows characteristic back-sloping as the soil establishes a new angle of repose along the margin of a gully that has been reclaimed by vegetation.

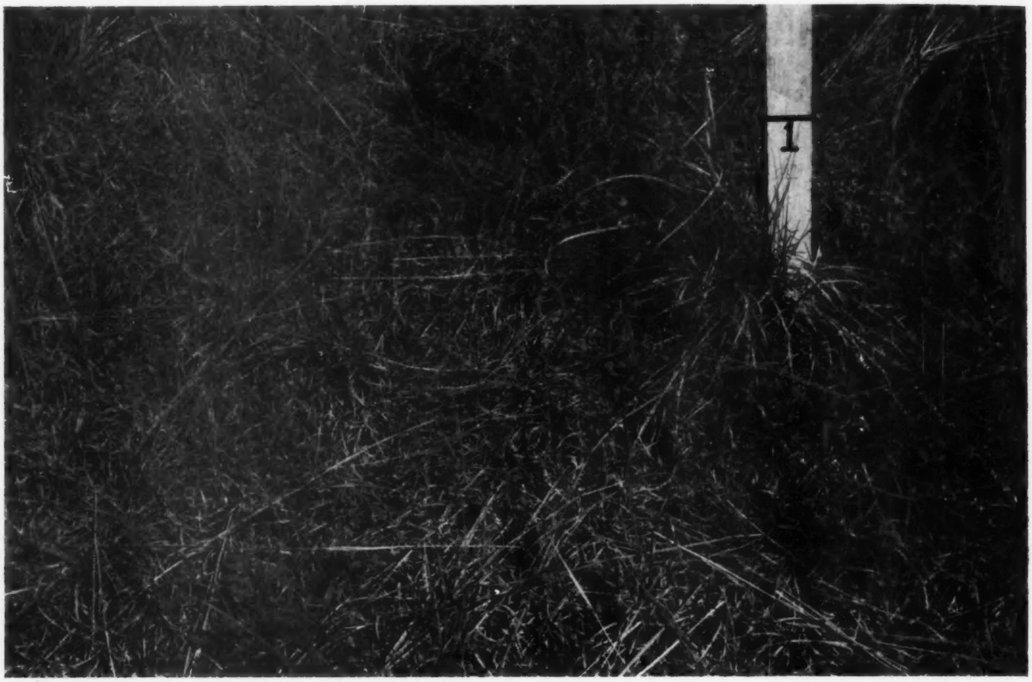


FIG. 30. A single plant of little bluestem with new growth about one foot tall in mid-April is shown in a lower dense cover of splitbeard bluestem. The earlier and taller growth of little bluestem may account for its ability to invade and displace the splitbeard bluestem stage.

in direct competition showed that little bluestem had a marked advantage in spring because of early superior height of foliage (Fig. 30).

When a few plants of little bluestem become established in the splitbeard bluestem stage, they soon form families over the field much as is shown in Figure 28. However, a subsere that includes a splitbeard bluestem stage may require more time than one where secondary succession proceeds directly from the threeawn to the little bluestem stage.

The little bluestem or final stage may be reached 14 years after abandonment. However, the final stage at first lacks many species of the climax community and differs from the original vegetation in other respects. Development to truly climax conditions is dependent upon the slow progress of soil formation, the arrival of propagules of lesser species of the climax, and spatial adjustments between climax species. The little bluestem or final stage of the subsere is shown in Figure 31.

Coverage by species in the little bluestem stage, illustrated in Figure 31, was as follows: little bluestem, 58 percent; splitbeard bluestem, 8 percent; yellow Indiangrass *(Sorghastrum nutans)*, 6 percent; Arrowfeather threeawn *(Aristida purpurascens)*, 3 percent; purple lovegrass, perennial lespedeza, sixweeks fescue, and western ragweed, each with 3 percent; and all others, 13 percent.

The findings here corresponded in many respects with findings in central Oklahoma by Smith (1940). There was startling similarity between stages of the subsere on abandoned fields of the Main Belt of Western Cross Timbers, and the subsere of abandoned fields in east-central Oklahoma and southeastern Kansas as reported by Booth (1941). The present findings differ markedly from Booth's in that *Quercus stellata* and *Q. marilandica* showed almost no tendency to re-enter abandoned fields. Furthermore, *Q. prinoides* was absent.

SUBSERE WITH UNRESTRICTED GRAZING

At the opposite extreme from old fields protected from grazing are those that have been consistently grazed to the extent of completely utilizing whatever forage was produced. Under unrestricted grazing the subsere is arrested in the threeawn stage, which, evidently, may persist indefinitely. Between the two extremes are various rates of succession.

An old field on which the subsere has been arrested in the threeawn stage for many years, becomes somewhat of a repository for all the least desirable forage species available to populate the area. This is the natural consequence of first exposing a bared area and then preventing establishment of all species except those which may escape grazing by low stature, or by reason of being unpalatable, or by short season of availability for grazing. Many annuals are notably

FIG. 31. The fourth or final stage of the subsere on old fields with little bluestem dominant. Fourteen years were required to reach the stage shown. The broad bladed grass is Indiangrass. Many species of the original vegetation are still absent, notably the oaks. Some species of earlier stages of the subsere are still present.

short-lived. There are many old fields in the Main Belt of the Western Cross Timbers on which grazing is unrestricted. Therefore, a detailed study of one was undertaken. A 45-acre field of a 52-acre farm, lying 4 miles northwest of Decatur, Texas, on U. S. Highway No. 81, was selected because it occupied typical Windthorst soils and its history was well known. The land was cleared and placed in cultivation in 1881. During the first 15 to 18 years yields of 480 to 500 pounds per acre of lint cotton and 60 bushels per acre of corn were common. About 1900 one gully formed but could be crossed with tillage implements. About 1905 the gully developed laterals and by 1915 sheet and gully erosion had destroyed the field for cropping purposes. The 52 acres supported one farm family for the brief span of about 35 years after which the family moved away. The gullies have enlarged since and sheet erosion continues under unrestricted grazing. Today no improvements or buildings are located there and the land is grazed by others (Fig. 32).

Data on the vegetation of the field shown in Figure 32 were obtained from mechanically spaced sample plots on both upper and lower slopes. Upper slopes had been abandoned 29 years and lower slopes between gullies had been abandoned 23 years at the time of sampling. Composition of vegetation on upper and lower slopes is given in Table 7.

The data in Table 7 show that annual threeawns were still dominant on both upper and lower slopes after two to three decades of abandonment and unrestricted grazing. The vegetation of upper slopes showed coverage of 20 percent by perennial grasses, 36 percent by annual grasses, 21 percent by perennial forbs, 20 percent by annual forbs, and 3 percent by woody species. On lower slopes the corresponding values were 13, 21, 24, 41, and 1 percent, respectively. Coverage by both perennial and annual grasses was greatest on upper slopes. Annual forbs were twice as abundant on lower slopes as on upper slopes. Annual grasses predominated on the upper slopes while annual forbs predominated on the lower slopes. Perennial grasses composed only 20 and 13 percent of coverage on upper and lower slopes, respectively. Table 7 provides a rather complete list of the species encountered on old fields of the Main Belt generally.

The gullies shown in Figure 32 supported a distinctive flora, largely because of inaccessibility to livestock but, no doubt, also because of other habitat differences. Samples showed 12 percent of total coverage by silver bluestem *(Andropogon saccharoides)*, 12 percent by narrowleaf bluets *(Houstonia angustifolia)*, and 8 percent by each of *Tragia ramosa*, *Gaura coccinea*, and *Lespedeza virginica*. Species each having 4 percent coverage were Johnsongrass, fall witchgrass, sand dropseed, Carolina horsenettle, western ragweed, and camphorweed. Johnsongrass was the only species limited to the gully walls. Evi-

Fig. 32. Aerial view of 45-acre old field. Extensive gully erosion is evident on the left of the square and sheet erosion on the right. The darker areas support annual threeawns after almost three decades of abandonment and unrestricted grazing.

dently it had been eliminated by grazing where accessible. Species that had greatest relative coverage on gully walls were generally those most palatable to livestock.

Subsere Assisted by Seeding

On some old fields the annual threeawn stage may persist for abnormally long periods even where protected from grazing. This condition was associated with absence in adjacent areas of successionally higher species, and therefore a source of seed. Trial seedings of native species had been made by employees of the U. S. Soil Conservation Service. Some of the earliest consisted of little more than introduction of the seed into the annual threeawn cover but grazing was properly managed after the seedings. Artificial revegetation may take the form of seed-bed preparation, control of competitors, possibly preliminary growing of a legume, or simple introduction of the seeds of successionally higher species and protection from grazing during the growing season of those species until they are established. The early work in artificial revegetation of the central and southern grasslands and advancements in techniques were ably reviewed by Savage (1939). Blake (1935) reported viability and germination of seeds and early life history of prairie plants. Cornelius (1946) reported methods of establishing many species found here, as well as coverage and yields for several years after reseeding. Daniel, Elwell, and Cox (1947) have reported extended studies in the Cross Timbers of Oklahoma with native grasses, particularly little bluestem. Included were consideration of methods of establishment, effects of fertilizer and cultivation on production of hay and seed, and yields of beef from revegetated eroded lands compared with cleared but uncultivated lands.

Though more elaborate techniques are now generally used, trials in the Western Cross Timbers have shown that it is possible to establish several climax grasses simply by introducing seeds into the annual threeawn stage of the subsere and then managing grazing. No seed-bed preparation was necessary. After the seed, or mature hay containing seed, was broadcast, the areas were gone over lightly with a disk. The disk was set to cut as little as possible. This procedure avoided loss of the small amount of organic matter that the threeawn stage had accumulated in the surface few inches, through root decay. It also avoided destruction of the surface layer of natural mulch. Kinds and amounts of natural mulches and their ecological significance have been reported by Dyksterhuis and Schmutz (1947). Seeding into a mulch left the threeawn community largely intact to compete with seedlings of the artificially introduced climax species. However, the possibility of the dis-

TABLE 7. Detailed composition and coverage by species on upper and lower slopes, 29 and 23 years, respectively, after abandonment of cultivated area to unrestricted grazing.

COMMON NAME	SCIENTIFIC NAME	COVERAGE	
		Upper Slopes	Lower Slopes
		Percent	*Percent*
(Perennial Grasses):			
Tumble lovegrass	Eragrostis sessilispica	7.59	....
Bermudagrass	Cynodon dactylon	3.80	....
Fringeleaf paspalum	Paspalum ciliatifolium	3.16	3.08
Red threeawn	Aristida longiseta	1.27	....
Silver bluestem	Andropogon saccharoides	1.01	1.92
Gummy lovegrass	Eragrostis curtipedicellata	.89	....
Texas grama	Bouteloua rigidiseta	.76	....
Sand dropseed	Sporobolus cryptandrus	.63	.14
Splitbeard bluestem	Andropogon ternarius	.38	6.30
Fall witchgrass	Leptoloma cognatum	.25	1.03
Mourning lovegrass	Eragrostis lugens	.13	....
Grasslike plants	Cyperus and Juncus spp.	....	.17
Other perennial		....	.17
(Annual Grasses):			
Kearney threeawn and Prairie threeawn	Aristida intermedia and Aristida oligantha	33.16	18.97
Sixweeks fescue	Festuca octoflora	3.04	2.47
Prairie trisetum	Trisetum interruptum	.13	....
(Perennial Forbs):			
Western ragweed	Ambrosia psilostachya	4.43	14.58
Dotted gayfeather	Liatris punctata	3.29	2.60
Rosemary falsesunrose	Helianthemum rosmarinifolium	2.53	.21
Carolina horsenettle	Solanum carolinense	2.28	.27
Narrowleaf bluets	Houstonia angustifolia	2.28	2.19
Scarlet gaura	Gaura coccinea	1.90	....
Yellow neptunia	Neptunial utea	1.39	....
Prairie acacia	Acacia angustissima	1.27	....
Western indigo	Indigofera leptosepala	.63	....
Longleaf eriogonum	Eriogonum longifolium	.51	....
Narrowleaf gromwell	Lithospermum angustifolium	.38	.21
Slender verbena	Verbena halei	.13	1.03
Common yellow oxalis	Oxalis stricta	....	.58
Sheep sorrel	Rumex acetosella	....	.34
Sand dozedaisy	Aphanostephus skirrobasis	....	.34
Berlandier goldaster	Chrysopsis berlandieri	....	.33
Wavyleaf thistle	Cirsium undulatum	....	.21
Slender lespedeza	Lespedeza virginica	....	.21
Noseburn	Tragia ramosa	....	.07
Dayflower	Commelina sp.	....	.07
Hairy pinweed	Lechea villosa	....	.03
Other perennial		....	.30
(Annual Forbs):			
Lanceleaf gaillardia	Gaillardia lanceolata	6.33	6.85
Rough buttonweed	Diodia teres	4.43	12.67
Camphorweed	Heterotheca subaxillaris	1.90	9.11
Annual plantains	Plantago spp.	1.39	2.40
Prairie rosegentian	Sabatia campestris	1.27	.86
Leastdaisy	Chaetopappa asteroides	.89	2.40
Showy partridgepea	Chaemaecrista fasciculata	.89	1.03
Rough falsepennyroyal	Hedeoma hispida	.63	.21
Slender fleabane	Erigeron strigosus	.63	....
Blackeyedsusan	Rudbeckia hirta	.25	1.34
Little bedstraw	Galium virgatum	.25	....
Spotted beebalm	Monarda punctata	.13	1.50
Southwestern carrot	Daucus pusillus	....	1.10
Pepperweed	Lepidium sp.	....	.75
Deervetch	Lotus americanus	....	.27
Common sunflower	Helianthus annuus	....	.21
Venuslookingglass	Specularia perfoliata	....	.07
Juniperleaf	Loeflingia texana	....	.14
Spotted euphorbia	Euphorbia maculata	....	.07
Drummond St. Johnswort	Hypericum drummondi	....	.07
(Annual Forbs, Cont.)			
Spermolepis	Spermolepis divaricatus	....	.07
All other annual forbs		.63	.[illegible]8
(Woody Plants):			
Carolina snailseed	Cocculus carolinus	2.53	....
Arkansas yucca	Yucca arkansana	.63	....
Common persimmon	Diospyros virginiana	....	.68
TOTALS		100.00	100.00

advantages of such competition being offset by advantages of a natural mulch should be considered on individual soils. The outcome of a seeding without seed-bed preparation is shown in Figure 33.

The bands where little bluestem was seeded are evident in Figure 33 because the darker old foliage contrasts with the lighter colored foliage of unseeded bands of annual threeawn. The range was grazed only in winter. The lower level of the bands of little bluestem is traceable to their being grazed while the alternate bands of threeawn were avoided. Annual threeawn appeared to be competing vigorously with little bluestem during the first and second years after seeding. However, by the fourth year little bluestem had eliminated the threeawns in the seeded areas, through competition for soil moisture. Furthermore, it had established scattered plants in the unseeded bands of annual threeawn.

Indiangrass has been established in a similar manner on lowland and big bluestem *(Andropogon furcatus)*, a tall grass with high moisture requirements, has been similarly established on upland (Fig. 34).

The big bluestem in Figure 34 is shown beyond the annual threeawn cover in which it was seeded. It is of interest that the stand has not yet produced a crop of seed. The stand is sufficiently dense to completely cover the ground but apparently the infertility of the old field soil, combined with the density of the stand, has thus far prevented production of flowering culms over the area generally.

FEATURES OF VEGETATION ASSOCIATED WITH MONTHS OF YEAR

Vegetation in a prairie climate exhibits striking differences in appearance from week to week or month to month. Through the growing season there are almost continuous changes as waves of different species reach their zenith of growth for the year. In winter there are obvious changes resulting from the different rates at which the different species are leached of color and disintegrate, as well as less obvious changes near the ground-line. The sequence and the genera involved have much in common throughout the north to south extent of the midcontinental prairies. The differences in the sequence may be appreciated by comparing the reports of Harvey

FIG. 33. Little bluestem hay with mature seeds was scattered on the darker colored band at the left four years before the picture was taken. The entire old field was then in the annual threeawn stage. The lighter colored unseeded band at the right shows the appearance of the original condition. It is still in the annual threeawn stage whereas threeawns have been eliminated by moisture competition in the seeded strip.

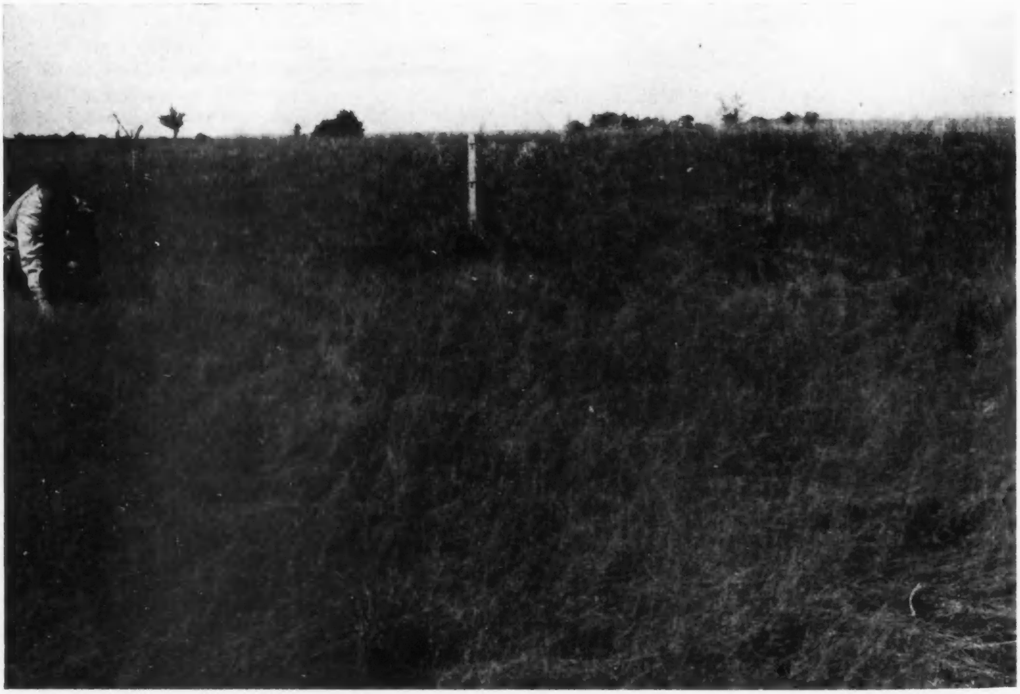


FIG. 34. Foreground shows the type of annual threeawn cover into which big bluestem (*Andropogon furcatus*) seed was scattered and lightly disked 5 years earlier. The resulting dense cover of big bluestem and elimination of threeawn is shown in the background.

(1908) from southeastern South Dakota or of Leopold and Jones (1947) from Wisconsin, of Steiger (1930) from Nebraska, and of Dyksterhuis (1946) from northcentral Texas. These references show variations through 10 degrees of latitude and will introduce additional literature on the subject.

An account of the seasonal development of the vegetation of an area has many applications in range management. Satisfactory results from pasture mowing, deferred grazing, rotation grazing, prescribed burning, reseeding, seed harvesting, diagnoses of causes for livestock gains and losses in weight, or deaths from plant poisoning all depend upon accurate knowledge of the stage of growth and composition of vegetation on a range at a certain time. Such knowledge is also applied to determine proper grazing periods (Costello & Price 1939). A report of the monthly sequence of development of vegetation provides an appropriate place to record subdominants which, though relatively unimportant from the standpoint of year-round vegetal cover, may, nonetheless, be quite important seasonally either as cover, or as forage, or as indicators of habitat differences. Furthermore, a list of the species of a local area, showing the stage of development in which each species is likely to be encountered in certain months, is of considerable help in field identification.

The data on growth and development of vegetation were obtained by making trips along a predetermined course with stops at six selected tracts between Alvord and Decatur, Texas. Field data were recorded at the middle of each month from February 1944 to February 1945. The species reported here are those that occurred on non-calcareous soils typical of the Main Belt of the Western Cross Timbers. Vegetation on local bodies of calcareous soils had virtually the same species and seasonal development as already reported for the Fort Worth Prairie (Dyksterhuis 1946).

Random checks on the data were made in various months in 1945 and 1946. From these it appeared that an event recorded in the middle of a month in 1944 may be expected to occur at some time within that same month each year. The data are therefore presented by months rather than by more specific dates.

In January the vegetation appeared dormant but closer examination showed several species which had considerable green foliage despite hard frosts. On pastures all species with some green foliage were sought by livestock. Non-dormant perennial grasses and grasslike plants included tumble lovegrass *(Eragrostis sessilispica)*, mourning lovegrass *(E. lugens)*, yellowsedge bluestem *(Andropogon virginicus)*, red threeawn *(Aristida longiseta)*, purple threeawn *(A. purpurea)*, Scribner panicum *(Panicum scribnerianum)*, Texas bluegrass *(Poa arachnifera)*, Canada wildrye *(Elymus canadensis)*, and the most common upland sedge of the area, *Carex microrhyncha* Mack. or smallsnout sedge. On very localized areas of fertile but much disturbed soil, a number of annual grasses were 2 to 4 inches tall. The principal species were Japanese brome *(Bromus japonicus)*, rescue brome *(B. catharticus)*, little barley *(Hordeum pusillum)*, and six-weeks fescue *(Festuca octoflora)*. The fresh green color of winter rosettes of numerous forbs was conspicuous beneath the generally dead cover of the preceding year's growth. Perennial or biennial species of forbs with winter rosettes included hairy pinweed *(Lechea villosa)*, Drummond pinweed *(L. drummondi)*, slender verbena *(Verbena halei* Small), wavyleaf thistle *(Cirsium undulatum)*, lanceleaf gaillardia *(Gaillardia lanceolata)*, low poppymallow *(Callirhoe involucrata)*, and *Solidago nitida* Torr. and Gray, or shiny goldenrod. Small rosettes of annual plantains (*Plantago* spp.) were numerous on greatly disturbed soils, such as recently abandoned fields and heavily stocked pastures. Other forbs with green shoots were spotted beebalm *(Monarda punctata)* and aromatic aster *(Aster oblongifolius)*.

In February several species were in flower, including smallsnout sedge of uplands, and American elm *(Ulmus americana)* and American plum *(Prunus americana)* of lowlands. Also, henbit deadnettle *(Lamium amplexicaule)*, tiny bluets *(Houstonia minima)*, Carolina anemone *(Anemone caroliniana)*, and species of *Draba*. Species observed germinating in February included southwestern carrot *(Daucus pusillus)*, dotted gayfeather *(Liatris punctata)*, and Kearney threeawn *(Aristida intermedia)*. Though several species, as noted, were in flower or germinating, the dominants of the overstory, namely, post oak *(Quercus stellata)*, and blackjack oak *(Quercus marilandica)* were still completely dormant as were also smooth sumac *(Rhus glabra)*, roughleaf dogwood *(Cornus asperifolia)* and species of *Celtis* or hackberry.

In March several additional species were flowering, including: boxelder *(Acer negundo)*, Chickasaw plum *(Prunus angustifolia)*, skunkbush sumac *(Rhus trilobata)*, mourning lovegrass, rescue brome, purple threeawn, red threeawn, Johnnyjumpup *(Viola kitaibeliana* var. *rafinesqui)*, western dwarfdandelion *(Krigia occidentalis)*, bigleaf pussytoe *(Antennaria plantaginifolia)*, Nuttall onion *(Allium nuttalli)*, and yellow falsegarlic *(Nothoscordum bivalve)*. A great number of herbaceous perennials broke winter dormancy in March. On March 15, 1944, purpletop *(Triodia flava)* was 1 inch tall, broadleaf uniola *(Uniola latifolia)* had shoots 3 inches tall, while western ragweed *(Ambrosia psilostachya)* and upright prairie-coneflower *(Ratibida columnaris)* were 2 inches tall. New shoots of the very common slender lespedeza *(Lespedeza virginica)* were 1 to 2 inches tall. Among woody plants, coralberry *(Symphoricarpos orbiculatus)*, roughleaf dogwood, and American elm showed new leaves one-half inch long. Germinating in March were prairie threeawn *(Aristida oligantha)*, snow-on-the-prairie *(Euphorbia bicolor* Engelm.), slender lespedeza, sessile tickclover *(Desmodium sessilifolium)*, and post oak, though some seedlings of the latter already had primary tap roots 10 or more inches long.

In April additional species were flowering, including white honeysuckle *(Lonicera albiflora)*, saw

greenbrier *(Smilax bonanox)*, post oak, blackjack oak, little barley, Texas bluegrass, Scribner panicum, tumblegrass *(Schedonnardus paniculatus)*, spiderworts (*Tradescantia* spp.), blue-eyedgrasses (*Sisyrinchium* spp.), violet woodsorrel oxalis *(Oxalis violacea)*, common yellow oxalis *(O. stricta)*, leastdaisy *(Chaetopappa asteroides)*, pinnate tansymustard *(Descurainia pinnata)*, narrowleaf gromwell *(Lithospermum angustifolium)*, slender bladderpod *(Lesquerella gracilis)*, Carolina geranium *(Geranium carolinianum)*, low poppymallow, *Hymenopappus* spp., Dakota verbena *(Verbena bipinnatifida)*, slender verbena, falsedandelion (*Pyrrhopappus* sp.), redseed plantain *(Plantago rhodosperma)*, halfshrub sundrops *(Oenothera serrulata)*, cutleaf gaura (*Gaura sinuata* Nutt.), greenthread (*Thelesperma trifidum* (Poir.) Britton), noseburn *(Tragia ramosa)*, Carolina horsenettle *(Solanum carolinense)*, and green antelopehorn *(Asclepiodora viridis)*. Species in flower, generally, were Nuttall onion, six-weeks fescue, and rescue brome. The common persimmon *(Diospyros virginiana)*, and pecan *(Carya illinoensis)* had just broken dormancy. Species observed germinating in April included oneseed croton *(Croton monanthogynus)*, Texas croton *(C. texensis)*, green croton *(C. glandulosus)*, rough buttonweed *(Diodia teres)*, horseweed fleabane *(Erigeron canadensis)*, showy partridgepea *(Chaemaecrista fasciculata)*, and puffsheath dropseed *(Sporobolus neglectus)*. This entire group of annuals are common invaders of depleted range land. They may be called summer annuals since they become prominent in summer after spring annuals have waned.

In May the flowers of several additional forbs were observed, including: slender fleabane *(Erigeron strigosus)*, wavyleaf thistle, Berlandier goldaster *(Chrysopsis berlandieri)*, butterfly milkweed *(Asclepias tuberosa)*, grooved flax *(Linum sulcatum)*, lanceleaf gaillardia, plains larkspur *(Delphinium virescens)*, Arkansas yucca *(Yucca arkansana)*, common poisonivy *(Toxicodendron radicans)*, clasping venuslookinglass *(Specularia perfoliata)*, oldfield toadflax *(Linaria canadensis)*, western indigo *(Indigofera leptosepala)*, and narrowleaf bluets *(Houstonia angustifolia)*. The most prominent flowers on the landscape were purplish patches of low poppymallow, whitish patches of hymenopappus, fragrant from a distance, blue spikes of slender verbena, yellow patches of half-shrub sundrops, and on old fields, great grayish patches made up of the hairy immature spikes of woolly Indianwheat *(Plantago purshi)* and bottlebrush Indianwheat *(Plantago aristata)*. Both of the latter flowered in May. Both are associated with extreme deterioration of the vegetation or of the soil or of both. Three perennial lovegrasses exserted first panicles in May. They were tumble, red, and purple lovegrasses (*Eragrostis sessilispica*, *E. secundiflora*, and *E. spectabilis*). Several grasslike plants common on uplands of the Cross Timbers were in flower and fruit. They were *Fimbristylis castanea* (Michx.) Vahl, *Cyperus ovularis* var. *sphaericus* Boeckl., *Cyperus filiculmis* Vahl, and *Juncus brachyphyllus* Wieg. The author's collection of the last named was the first record of the species in Texas.

In June numerous early species had ceased flowering. Some were developing fruits, while others had already disseminated their seeds and had virtually disappeared. Meanwhile still other species were just beginning to blossom. Fruits of the native Chickasaw plum and the southern dewberry *(Rubus trivialis)* were ripe and common. Peach trees at abandoned farmsteads also bore some ripe fruit. Grasses beginning to flower included sand dropseed *(Sporobolus cryptandrus)*, fringeleaf paspalum *(Paspalum ciliatifolium)*, fall witchgrass *(Leptoloma cognatum)*, Bermudagrass *(Cynodon dactylon)*, sideoats grama *(Bouteloua curtipendula)*, and jointtail *(Manisuris cylindrica)*. Grasses generally in flower in June included: mat sandbur *(Cenchrus pauciflorus)*, silver bluestem *(Andropogon saccharoides)*, splitbeard bluestem *(A. ternarius)*, Johnsongrass, tumble lovegrass, gummy lovegrass *(Eragrostis curtipedicellata)*, red lovegrass, knotroot bristlegrass *(Setaria geniculata)*, Canada wildrye, and Virginia wildrye *(Elymus virginicus)*. Grasses that had matured inflorescences before or in mid June included Texas bluegrass, Scribner panicum, Texas grama *(Bouteloua rigidiseta)*, tumblegrass, mourning lovegrass, and tumble windmillgrass *(Chloris verticillata)*. In June, forbs with yellow flowers included showy partridgepea, camphorweed *(Heterotheca subaxillaris)*, upright prairieconeflower, spotted beebalm, yellow neptunia *(Neptunia lutea)*, blackeyedsusan *(Rudbeckia hirta)*, Rosemary falsesunrose *(Helianthemum rosmarinifolium)*, fourpoint sundrops (*Oenothera rhombipetala* Nutt.), and star-of-Texas *(Xanthisma texanum)*. Forbs with blue or purple flowers included dayflower (*Commelina* sp.), longleaf scurfpea *(Psoralea linearifolia)*, sessile tickclover, and Carolina horsenettle. Forbs with white or whitish flowers included prairie dogbane *(Apocynum sibiricum)*, prairie acacia *(Acacia angustissima)*, sand dozedaisy *(Aphanostephus skirrobasis)*, and juniperleaf *(Polypremum procumbens)*. Forbs with red to pink flowers included prairie rosegentian *(Sabatia campestris)*, trailing scurfpea *(Psoralea rhombifolia)*, Spanishclover deervetch *(Lotus americanus)*, bigtop dalea *(Dalea enneandra)*, and rough buttonweed.

In July a few additional forbs with yellow flowers were evident. Included were common sunflower *(Helianthus annuus)*, Drummond St. Johnswort *(Hypericum drummondi)*, and Carolina snailseed *(Cocculus carolinus)*. Forbs with blue to purple flowers included slender lespedeza, trailing lespedeza *(Lespedeza procumbens)*, Stuves lespedeza *(L. stuvei)*, Texas milkpea (*Galactia texana* A. Gray), and small wildbean *(Strophostyles pauciflora)*, all of the legume family. Also the composite, Baldwin ironweed *(Vernonia baldwini)*. Three weedy forbs that began to show small greenish flowers were western ragweed *(Ambrosia psilostachya)*, green croton, and slender copperleaf *(Acalypha gracilens)*. Several species were shedding seed in July, including: Drummond pinweed and the taller hairy pinweed, upright prairie-

coneflower, purple threeawn, red threeawn, knotroot bristlegrass, mat sandbur, sand dropseed, and *Juncus marginatus* var. *setosus* Coville. It is of interest that a single five-acre old field of typical eroded sandy noncalcareous Cross Timbers soils, long protected from grazing, contained 15 species of native legumes that ripened some seeds before the end of July. The species were: prairie acacia, showy partridgepea, Spanishclover deervetch, yellow neptunia, Texas milkpea, longleaf scurfpea, trailing scrufpea, three lespedezas (slender, Stuves, and trailing), sessile tickclover, small wildbean, bigtop dalea, arrow crotalaria *(Crotalaria sagittalis)*, and pencilflower *(Stylosanthes biflora)*.

In August the drought which usually characterizes late July and August had become acute. However, the yellow to orange flowers of shiny goldenrod *(Solidago nitida)* and *Berlandiera dealbata* (Torr. & Gray) Small, appeared locally. Most conspicuous on roadsides were common sunflower, snow-on-the-prairie, and blood ragweed *(Ambrosia aptera)*. The ordinary overgrazed pasture presented an almost continuous cover of western ragweed which now overtopped inherently smaller species as well as more palatable and hence closely grazed species of taller habit.

In September virtually all vernal species had ceased flowering and spring annuals had shriveled leaving scarcely a trace. Fall flowering species were coming into prominence, including: aromatic aster and purple gerardia *(Gerardia purpurea)* which had begun to flower. The violet woodsorrel oxalis, yellow false-garlic, sideoats grama, fall witchgrass, and silver bluestem began their second period of flowering for the year, as they do each year. Grasses with inflorescences newly exserted included: hairy grama *(Bouteloua hirsuta)*, blue grama *(B. gracilis)*, purpletop *(Triodia flava)*, tall dropseed *(Sporobolus asper)*, sand lovegrass *(Eragrostis trichodes)*, Indiangrass *(Sorghastrum nutans)*, and switchgrass *(Panicum virgatum)*. Details concerning seasonal development of little bluestem *(Andropogon scoparius)* and of other major dominants are given in the section on autecology.

In October the whitish flowers appeared on sageworts (herbaceous *Artemisia* spp.), heath aster *(Aster ericoides)*, and on manyflowered eriogonum *(Eriogonum multiflorum)*. The last may be classed as an index species for deep coarse-textured soils. On overgrazed pastures the numerous small yellow flowers of the annual snakeweed or "broomweed" *(Gutierrezia dracunculoides)* became a dominant feature. The acorns of post oak and blackjack oak were falling. Leaves of several species had turned red. Conspicuous were those of smooth sumac, flameleaf sumac (*Rhus lanceolata* A. Gray), Virginia creeper *(Parthenocissus quinquefolia)*, common poisonivy and slender copperleaf. The carmen fruits of Carolina snailseed adorned many fence-rows where protected from grazing. Many herbaceous species were developing fresh green winter rosettes at the surface of the ground. Most common were the rosettes of Scribner panicum, hairy pinweed, Drummond pinweed, slender verbena, wavyleaf thistle, lanceleaf gaillardia, low poppymallow, and shiny goldenrod. Many common species characteristically germinated in the fall. Species observed germinating in October included Texas grama, rescue brome, Japanese brome, little barley, sixweeks fescue, redseed plantain and woolly Indianwheat.

In November the leaves of the oaks had turned brown. The species that had red leaves a month earlier were now leafless. The only evident blossoms were those on occasional plants of camphorweed and showy partridgepea. On many old fields the white-hairy inflorescences of splitbeard bluestem were most conspicuous. Several species were going into complete winter dormancy, including western ragweed, big bluestem, silver bluestem, red lovegrass, sand lovegrass, switchgrass, Johnsongrass, purpletop, fringeleaf paspalum, and broadleaf uniola.

In December the largest and oldest post oaks had shed their leaves but young specimens and blackjack oaks retained most of the dried leaves. Occasional willow trees along drainages still had some green leaves while on uplands green leaves were still conspicuous on woollybucket bumelia *(Bumelia lanuginosa)*, common mesquite *(Prosopis juliflora)*, and coralberry. Two common woody plants of the Cross Timbers appeared to retain some green leaves throughout the year. These partially evergreen species were saw greenbrier *(Smilax bonanox)*, and southern dewberry *(Rubus trivialis)*. Numerous grasses which appeared dormant from a distance had green sheaths and blades within the clumps of dead material, throughout the winter. In general, the native grasses which regularly become dormant in winter did so in November, even in advance of killing frosts. In contrast, the two most common introduced and escaped pasture grasses, namely, Johnsongrass and Bermudagrass, continued active growth and retained much green foliage until frosts evidently forced them into dormancy.

Weaver and Clements (1938) have stated that the adjustment of species to seasonal changes results in what are called aspects, the adjustment being another of several ways in which the vegetation of an area may show structure. The foregoing account scarcely qualifies as an account of seasonal aspects or of characteristic societies in the sense of describing structure of one or more natural units of vegetation. The data are not related to specific climax or seral units of vegetation, but rather were gathered from the mosaic of greatly and variously disturbed remnants of the original vegetation as they occur today. Also, the account will scarcely qualify as phenology since the dates of events are not recorded but rather only the months in which obvious features of the landscape were observed. It is hoped that the data presented may stimulate sufficient interest in the flora and find sufficient application in range management practices to result in phenologic studies and studies of the aspects that characterize specific seral and climax units.

DISCUSSION

Discussions of results have been included under individual headings insofar as possible. Discussion of the "climax-problem" has been left to the last where all findings may be drawn upon.

Weaver and Clements (1938) stated that the Cross Timbers are to be regarded as oak savannah in which the grasses are climax dominants. Quantitative data and historical records given in preceding sections corroborate this conclusion. Furthermore, the data show that where the grasses have been reduced by overgrazing, the density of the stand of oaks increases to a point where the vegetation becomes oak forest or woodland rather than savannah. Today, stands of oak woodland are more prevalent than savannah throughout the Main Belt. The present vegetation, therefore, is regarded as disclimax oak woodland. The increase in coverage by woody species is attributed to reduction in competition for moisture once provided by perennial herbaceous species whose coverage was disproportionately reduced under overgrazing by domestic livestock which grazed the herbaceous perennials over the longest period each year.

Fire was, no doubt, a factor in the maintenance of the original savannah but today intensive grazing largely prevents accumulation of sufficient fuel. This, too, favors post oak and blackjack oak rather than the grasses. Young sprouts and seedlings of the oaks extend their crowns up out of reach of grazing animals within a decade or less and soon have enough bark to withstand the puny ground fires which the limited amounts of dead materials occasionally permit. Great quantities of fuel and occasional hot fires of the original savannah must repeatedly have killed sprouts and young trees back to the ground-line where the new shoots were once again forced to compete on more nearly equal terms with the new growth of the grasses. Moreover, their entire photosynthesizing surface was again placed within reach of grazing animals. Animals prefer the leaves of sprouts because of their greater succulence. Secondary succession without fire or clearing does not restore the original savannah condition shown in Figures 15 and 16, but rather a condition comparable to that shown in Figures 20 and 21. Occasional fires with abundant fuel, therefore, are regarded as a part of climax conditions in accepting grasses as the climax dominants.

Weaver and Clements (1938) stated, "In this prairie climate, the oaks constitute a postclimax, since the climax forest would return in the event of a shift to a wetter climate." Evidence is also provided of earlier occupancy by forest (Clements 1936), and the postclimax nature of the overstory of oaks is accepted. The fact that the grasses are climax dominants of the understory, however, has led to occasional reference to "climax vegetation" of the Western Cross Timbers. Such references are not intended to conflict with the climatic climax theory nor with acceptance of the concept of the postclimax nature of the oaks in this climate. They refer, rather, to the final stage of plant succession, in the absence of abnormal disturbance, on soils long formed.

The question of whether or not the Western Cross Timbers are actually within a grassland climate received considerable study. The zonal or climatic Great Soil Groups described by Kellogg (1936) and others are not fully reconciled with the climatic climax plant formations of Weaver and Clements (1938), or with climates as described by Thornthwaite (1931, 1941) who also considered vegetation. Furthermore, there is some evidence that changes in climate at the boundary of the Deciduous Forest formation of the eastern United States and the mid-continental Grassland formation have occurred in quite recent geologic time and that these formations are now adjusting their boundaries. A comprehensive discussion of this subject will not be attempted, though some findings and their implications, as they apply to the Western Cross Timbers, will be considered.

Mature Reddish Prairie soils are regarded as zonal or climatic soils by soil scientists (Kellogg 1936, U. S. Department of Agriculture Yearbook 1938). Such soils are found in large bodies along the western side of the Fringe as well as in small bodies throughout the area under study, where they are known as "included prairies." Their original cover was open grassland. Such soils characteristically are found on "flats." The almost level relief, in conformity with the concepts of Jenny (1941), provides additional evidence of full effect of soil forming factors. If these mature Reddish Prairie soils reflect a full response to climate and have not been and are not now invaded by oaks except under disturbance, then the climate of the entire area would be indicated to be still that of grassland. The point is worth considering in light of the conclusion by McComb and Loomis (1944) that much of the prairie peninsula of Iowa and Illinois (also within the area of zonal Prairie soils) is a subclimax associes and that the oak-hickory forest is climax under present climatic conditions. In partial support of their conclusion they point out that Iowa forests survived the recent great drought without injury and that they are spreading. Gates (1939) found westward migration of at least 31 species of trees in Kansas since settlement but post oak and blackjack oak were not among them. Harper (1940) reported death of trees in relation to soils and climate in the southern Great Plains, particularly in Oklahoma. Albertson and Weaver (1945) monographed effects of drought upon trees in a prairie climate. The areas within the Cross Timbers where numerous trees were killed by the recent great drought are shown on the map (Fig. 1). The appearance of such areas is shown in Figure 35. Death from drought and the virtual absence of invasion on undisturbed mature Reddish Prairie soils and on abandoned fields support the conclusion that the situation here differs from that of the prairie peninsula and that the climate is still that of grassland. Furthermore, following the concepts of Kellogg (1936) and Jenny (1941) regarding soil formation, and those of Weaver and Clements (1938) regarding climatic climaxes, it may be concluded that under existing climate the Fringe

of the Cross Timbers should develop mature Reddish Prairie soils in geologic time with virtual elimination of the overstory of postclimax oaks. As indicated by Jenny (1941) soil maturity might be expected to occur in conjunction with geologic erosion which would ultimately give the present rugged surfaces of immature soils a relief comparable to that of existing interspersed bodies of Reddish Prairie soils.

FIG. 35. The dead oaks were killed by the great drought of the 1930's. This area is one of many shown in Figure 1, in the Fringe of the Cross Timbers, where oaks were killed by the great drought. The area shown has been grazed conservatively since the drought and a good stand of herbaceous perennials has developed. The absence of tree reproduction among the dead trees is noteworthy. *(Photo. by Mack McConnell.)*

The podzolic character of the soils of the Main Belt is scarcely to be ascribed to the present climate because the area lies well within the area of zonal prairie soils delineated by Kellogg (1936). The soil character may be attributed to the effect of the high sand content of the parent material which permitted abnormally great leaching. Such leaching may have occurred in times of greater precipitation when climax oak forest was also present, or it may still be occurring today. In the light of the data on climate and vegetation, and considering interspersed Reddish Prairie soils, it appears improbable that Red and Yellow Podzolic soils are being developed in this area under the present climate. If they are not, then the Main Belt of the Western Cross Timbers must possibly be regarded as a great body of soils of podzolic origin, now not readily classifiable. The relations between climax units of vegetation and zonal soils are believed to be a fruitful field for additional study by ecologists and pedologists. The Cross Timbers should probably receive high priority for such studies.

SUMMARY AND CONCLUSIONS

1. Sample plots at one-fifth mile intervals along 76 miles of cross-country transects, as well as hundreds of plots on scores of tracts selected for special study, were analyzed during 9 years. They provided data on coverage by species over broad areas as well as under selected environmental influences. These data were supplemented by data acquired at monthly intervals through one year.

2. The boundary of the Western Cross Timbers and its major divisions were determined and mapped. The area was found to consist of a Main Belt of sandy soils with gentle relief developed upon Cretaceous outcrops covering 2,436,000 acres, and a Fringe of rocky and gravelly soils with rough relief developed upon Pennsylvanian outcrops covering 1,680,000 acres. Both divisions are characterized by a sparse overstory of post oak *(Quercus stellata)* and blackjack oak *(Q. marilandica)*.

3. An attempt was made to locate and review all pertinent accounts of the vegetation from earliest Caucasian influence through the peak of occupation by farmers which is now giving way to ranching. Early accounts were oriented with present place-names and conditions.

4. Basic knowledge of the climate, geology, and soils of the area is summarized. Grazing influences, woodland conditions and forestry, and fire are considered in their relation to present vegetation. Cultivation, crops, and erosion are considered in relation to changing use of the land and vegetation since settlement.

5. Present understory vegetation is a grazing disclimax in which annual forbs predominate. In the order of decreasing relative coverage, the species or groups are ranked as follows: annual forbs, 19 percent; *Buchloe dactyloides* or buffalograss, 9 percent; the two oaks, 7 percent; annual *Aristida* spp. or threeawns, 6 percent; *Bouteloua hirsuta* or hairy grama, 5 percent; and some 20 other species, which each compose less than 5 percent but over 0.5 percent of total coverage.

6. The understory vegetation of the Main Belt differs from that of the Fringe. Buffalograss is four times as abundant in the latter. The oaks, *Paspalum ciliatifolium*, annual threeawns, hairy grama, *Andropogon saccharoides*, and *Smilax bonanox* are far more abundant in the Main Belt. Some 30 species with coverage of over 0.3 percent in one division show different or virtually no coverage in the other division.

7. Physiognomy of the vegetation is associated with certain classes of soils. Floristically there are four broad types of vegetation. They are the *Quercus-Smilax* type of podzolic soils, the *Quercus-Prosopis* type of immature Reddish Prairie soils, the *Prosopis* type of mature Reddish Prairie soils, and the old-field type of podzolic soils that have been cleared, cultivated, and abandoned because of erosion. Coverage of over 0.2 percent is reported for some 50 species occurring in one or more of the types. Species and their relative coverage differ greatly by types.

8. Climax or original vegetation, as determined from relicts, consisted of the mid grass, *Andropogon scoparius*, as the major dominant and with the two tall grasses, *Sorghastrum nutans* and *A. furcatus*, as lesser dominants. Species composition of relict original vegetation is reported for two areas of each of the three soil groups at widely separated locations.

9. Differences between vegetation of the different soils are much greater now than they were originally. Little bluestem was a universal dominant of the climax but in the grazing disclimax the oaks predominate on podzolic soils, annual forbs on immature Reddish Prairie soils, and buffalograss on mature Reddish Prairie soils.

10. Grazing by domestic livestock was the primary cause of the modification of Cross Timbers vegetation. Basic knowledge of grazing as an ecological source of variation in vegetation is briefly reviewed.

11. Grazing coactions were determined by monthly studies of both grazing animals and range vegetation under three intensities of grazing. It was found that 60 species composed an important part of the diet of livestock on lightly to moderately stocked range land through the course of a year. The species chosen in different months were related to certain events in the phenology of the species selected. The principal part of the diet consisted of new shoots of woody plants in April, annual forbs in May, and perennial grasses in June. Native legumes composed an important part of the diet in July only. Winter rosettes were an important part of the diet from December to March. Months of light, moderate, and heavy use of species selected by livestock are shown to the nearest one-half month. Implications in range management here and in general are discussed.

12. Autecological studies of 14 of the most important grasses in the Western Cross Timbers are reported, particularly their monthly development and growth habits in relation to grazing. Included are studies of *Andropogon scoparius, Sorghastrum nutans, Bouteloua hirsuta, B. curtipendula, Sporobolus asper, Buchloe dactyloides, Aristida* spp. of the Group Purpureae, *Paspalum ciliatifolium, Stipa leucotricha, Andropogon saccharoides, Cynodon dactylon, Panicum scribnerianum*, five perennial species of *Eragrostis*, and *Andropogon ternarius* or splitbeard bluestem.

13. The course of range degeneration in the Main Belt and its effects on species composition of both overstory and understory was determined. Four typical points in degeneration, or range condition classes, are described and illustrated.

14. Subseres, or secondary succession, on abandoned fields varied, depending upon degree of grazing disturbance, proximity of a source of seed of successionally higher species, and the degree of erosion at the time the field was abandoned. The subsere on old fields with ordinary degree of erosion, protected from grazing and adjoining a source of seed, may reach the final stage in 14 years. There are typically four stages, namely, the weed stage, the annual threeawn stage, the splitbeard bluestem stage, and the little bluestem or final stage. The splitbeard bluestem stage is sometimes omitted. The development of the vegetation is described and illustrated.

15. With unrestricted grazing the subsere may be arrested in the annual threeawn stage for decades. During this period numerous species not otherwise present attain some coverage. These finally include virtually all species available to populate the area that can also persist despite intensive grazing. Species composition and history of one such area abandoned three decades is given in detail.

16. Subseres on old fields protected from grazing are commonly arrested in the annual threeawn stage for long periods because seeds of the next stage are lacking. This was proven where seeds of climax grasses had been simply scattered in bands several yards wide. On such bands the climax grasses completely eliminated the annual threeawns through moisture competition within four to seven years and volunteered in the adjacent cover of threeawns but not beyond a distance of about one-eighth mile and commonly less.

17. Features of the vegetation associated with months of the year are reported, including notes on: 13 species that did not go dormant in winter at this latitude and 10 that did; nine species with prominent winter rosettes and five common winter annuals; time of germination of 22 species; time of flowering of 133 species; and time of mature fruits on 39 species.

18. The "climax-problem" of the transition area between forest and prairie is discussed insofar as it applies to the Western Cross Timbers. It is concluded that the area is within a grassland climate though density of the stand of oaks has increased under overgrazing to a point where the landscape approaches that of forest or woodland rather than savannah.

LITERATURE CITED

Albertson, F. W., & J. E. Weaver. 1945. Injury and death or recovery of trees in prairie climate. Ecol. Monog. **15:** 393-433.

Archibald, J. G., E. Bennett, & W. S. Ritchie. 1943. The composition and palatability of some common grasses. Jour. Agri. Res. **66:** 341-347.

Bauer, H. L. 1943. The statistical analysis of chaparral and other plant communities by means of transect samples. Ecology **24:** 45-60.

Bennett, H. H. 1939. Soil Conservation. 993 pp. McGraw-Hill Book Co., Inc. New York and London.

Blake, A. K. 1935. Viability and germination of seeds and early life history of prairie plants. Ecol. Monog. **5:** 405-460.

Bolton, H. E. 1914. Athanase De Mezieres and the Louisiana-Texas frontier 1768-1780. 2 vols. Arthur H. Clark Co., Cleveland.
1915. Texas in the middle eighteenth century. Univ. Calif. Pubs. in History, Vol. 3. Univ. Calif. Press, Berkeley.

Bonnen, C. A., & B. H. Thibodeaux. 1937. A description of the agriculture and type-of-farming areas in Texas. Tex. Agri. Expt. Sta. Bul. **544.** 99 pp.

Bruner, W. E. 1931. The vegetation of Oklahoma. Ecol. Monog. **1:** 99-188.

Bullard, F. M., & R. H. Cuyler. 1930. A preliminary report on the geology of Montague County, Texas. Univ. Tex. Bul. **3001:** 57-76.

Bushnell, T. M., H. W. Hawker, & D. B. Pratapas. 1923. Soil survey of Erath County, Texas. U. S. Dept. Agr., Bur Soils, in coop. Tex. Agri. Expt. Sta. Pp. 371-406 and map.

Carter, W. T. 1931. The soils of Texas. Tex. Agr. Expt. Sta. Bul. **431**. 192 pp. and map.

Clements, F. E. 1916. Plant succession. Carn. Inst. Wash. Pub. **242**. 512.
1934. The relict method in dynamic ecology. Jour. Ecol. **22**: 39-68.
1936. Nature and structure of the climax. Jour. Ecol. **24**: 252-284.
1936. The origin of the desert climax and climate. In: Essays in geobotany in honor of William Albert Setchell, pp. 87-140. Univ. Calif. Press., Berkeley, Calif.

Clements, F. E., & V. E. Shelford. 1939. Bio-ecology. 425 pp. John Wiley and Sons, Inc., New York.

Cornelius, D. R. 1946. Establishment of some True Prairie species following reseeding. Ecology **27**: 1-12.
1947. The effect of source of Little Bluestem seed on growth, adaptation, and use in revegetation seedings. Jour. Agr. Res. **74**: 133-143.

Cory, V. L. 1927. Activities of livestock on the range. Tex. Agr. Expt. Sta. Bul. **367**. 47 pp.

Cory, V. L., & H. B. Parks. 1938. Catalogue of the flora of Texas. Tex. Agr. Expt. Sta. Bul. **550**. 130 pp.

Costello, D. F., & R. Price. 1939. Weather and plant-development data as determinants of grazing periods on mountain range. U. S. Dept. Agr. Tech. Bul. **686**. 31 pp.

Cuyler, R. H. 1931. Vegetation as an indicator of geologic formations. Amer. Assoc. Petroleum Geol. Bul. **15**: 67-78.

Daniel, H. A, H. M. Elwell, & M. B. Cox. 1947. Conservation and land use investigations. Okla. Agri. Expt. Sta. Bul. **B-309**. 32 pp.

Drew, W. B. 1942. The revegetation of abandoned cropland in the Cedar Creek area, Boone and Callaway Counties, Missouri. Univ. Mo., Coll. Agr., Agr. Expt. Sta. Res. Bul. **344**. 52 pp.

Duck, L. G., & J. B. Fletcher. 1943. A survey of the game and furbearing animals of Oklahoma (with unattached "Game type map of Oklahoma"). Div. of Wildlife Restoration and Res., Oklahoma. Game & Fish Coms., Pittman-Robertson Series II, State Bul. **3**. 144 pp. and map.

Dyksterhuis, E. J. 1945. Axillary cleistogenes in Stipa leucotricha and their role in nature. Ecology **26**: 195-199.
1946. The vegetation of the Fort Worth Prairie. Ecol. Monog. **16**: 1-29.

Dyksterhuis, E. J., & E. M. Schmutz. 1947. Natural mulches or "litter" of grasslands: with kinds and amounts on a southern prairie. Ecology **28**: 163-179.

Elwell, H. M., H. A. Daniel, & F. A. Fenton. 1941. The effects of burning pasture and woodland vegetation. Okla. Agr. Expt. Sta. Bul. **B-247** 14 pp.

Fraps, G. S., & V. L. Cory. 1940. Composition and utilization of range vegetation of Sutton and Edwards Counties. Tex. Agr. Expt. Sta. Bul. **586**. 39 pp.

Fraps, G. S., & J. F. Fudge. 1937. Chemical composition of soils of Texas. Tex. Agr. Expt. Sta. Bul. **549**. 87 pp.

Fudge, J. F., & G. S. Fraps. 1945. The chemical composition of grasses of northwest Texas as related to soils and requirements for range cattle. Tex. Agr. Expt. Sta. Bul. **669**. 56 pp.

Fulton, M. G. 1941. Diary and letters of Josiah Gregg; southwestern enterprises 1840-1847. 413 pp. Univ. Okla. Press. Norman, Okla.

Gates, F. C. 1939. Trends of tree migration in Kansas. Kansas Acad. Sci. Trans. **42**: 127-132.

Geiser, S. W. 1937. Naturalists of the frontier. 341 pp. Southern Methodist Univ. Press. Dallas, Texas.

Gray, A. Synoptical flora of North America: The gamopetalae. Smithsonian Miscl. Pub. **591**, Pt. 1, 480 pp. Pt. 2, 494 pp.

Harper, H. J. 1940. Relation of climatic conditions, soil characteristics, and tree development in the southern Great Plains region. Soil Sci. Soc. Amer. Proceed. **5**: 327-335.

Hart, G. H., H. R. Guilbert, & H. Goss. 1932. Seasonal changes in the chemical composition of range forage and their relation to nutrition of animals. Univ. Calif. Coll. Agr., Agr. Expt. Sta. Bul. **543**. 62 pp.

Harvey, L. H. 1908. Floral succession in the prairie-grass formation of southeastern South Dakota. Bot. Gaz. **46**: 81-108, 277-298.

Hill, R. T. 1887. The topography and geology of the Cross Timbers and surrounding regions in northern Texas. Amer. Jour. Sci., 3d Series, Vol. 33, No. 196, pp. 291-303.
1901. Geography and geology of the Black and Grand Praries, Texas. U. S. Geol. Surv., 21st Ann. Rept., Pt. 7, 666 pp.

Hitchcock, A. S. 1935. Manual of the grasses of the United States. U. S. Dept. Agr. Miscl. Pub. **200**. 1040 pp.

Jenny, H. 1941. Factors of soil formation. 281 pp. McGraw-Hill Book Co., Inc., New York and London.

Johnstone-Wallace, D. B., & K. Kennedy. 1944. Grazing management practices and their relationships to the behaviour and grazing habits of cattle. Jour. Agr. Sci. **34**: 190-197.

Kellogg, C. E. 1936. Development and significance of the great soil groups of the United States. U. S. Dept. Agr. Miscl. Pub. **229**. 40 pp.

Kelsey, H. P., & W. A. Dayton. 1942. Standardized plant names. 2d ed. 675 pp. J. Horace McFarland Co., Harrisburg, Pa.

Kendall, G. W. 1845. Narrative of an expedition across the great southwestern prairies. 2 vols. David Bogue, London.

Kennedy, W. 1841. The rise, progress, and prospects of the Republic of Texas. London. Reprinted in one volume by Molyneaux Craftsmen, Inc., Fort Worth, Texas. 1925.

Leopold, A., & S. E. Jones. 1947. A phenological record for Sauk and Dane Counties, Wisconsin, 1935-1945. Ecol. Monog. **17**: 81-122.

Lundell, C. L., et al. 1942, 1943, 1944. Flora of Texas. Vol. **3**: Pts. 1, 2, 3, and 4. 262 pp. to date. Southern Methodist Univ. Press, Dallas, Texas.

Marcy, R. B. 1849. His diary as Captain of 5th Infantry U. S. Army. 31st Cong., 1st Sess. 1849-50, U. S. Senate Exec. Doc., Vol. **14**, Nos. 64-82, pp. 204-220.

Marcy, Col. R. B. 1866. Thirty years of army life on the border. 442 pp. Harper & Bros., Franklin Sq., N. Y.

McBryde, J. B. 1933. The vegetation and habitat factors of the Carrizo sands. Ecol. Monog. **3**: 247-297.

McComb, A. L., & W. E. Loomis. 1944. Subclimax prairie. Bul. Torrey Bot. Club. **71**: 46-76.

Mueller, I. M., & J. E. Weaver. 1942. Relative drought resistance of seedlings of dominant prairie grasses. Ecology **23**: 387-398.

Osborn, B. 1943. Wildlife and habitats in Young Co., Texas, by a new method of survey. Jour. Wildlife Management **7**: 241-256.

Plummer, F. B., & R. C. Moore. 1921. Stratigraphy of the Pennsylvanian formations of north-central Texas. Univ. Tex. Bul. **2132**. 237 pp.

Savage, D. A. 1939. Grass culture and range improvement in the central and southern Great Plains. U. S. Dept. Agr. Circ. **491**. 56 pp.

Scott, G., & J. M. Armstrong. 1932. The geology of Wise County, Texas. Univ. of Tex. Bul. **3224**. 77 pp.

Sellards, E. H., W. S. Adkins, & F. B. Plummer. 1932. The geology of Texas. Vol. I. Stratigraphy. Univ. of Tex. Bul. **3232**. 1007 pp.

Small, J. K. 1903. Flora of the southeastern United States. 1370 pp. Pub. by author. New York.

Smith, A. D. 1944. A study of the reliability of range vegetation estimates. Ecology **5**: 441-448.

Smith, C. C. 1940. Biotic and physiographic succession on abandoned eroded farmland. Ecol. Monog. **10**: 421-484.
1940. The effect of overgrazing and erosion upon the biota of the mixed-grass prairie of Oklahoma. Ecology **21**: 381-397.

Smith, J. G. 1899. Grazing problems in the southwest and how to meet them. U. S. Dept. Agric., Div. Agrostol. Bul. **16**. 46 pp.

Steiger, T. L. 1930. Structure of prairie vegetation. Ecology **11**: 170-217.

Stemen, T. R., & W. S. Meyers. 1937. Oklahoma flora. 706 pp. Harlow Pub. Corp., Oklahoma City, Okla.

Stewart, G., & S. S. Hutchings. 1936. The point-observation-plot (square-foot-density) method of vegetation survey. Jour. Amer. Soc. Agron., **28**: 714-722.

Stiff, Col. E. 1840. The Texan emigrant. Pp. 40-41. George Conclin, Cincinnati.

Tharp, B. C. 1926. Structure of Texas vegetation east of the 98th meridian. Univ. Tex. Bul. **2606**. 100 pp.

Thornthwaite, C. W. 1931. The climates of North America according to a new classification. Geogr. Rev. **21**: 633-655.
1941. Atlas of the climatic types in the United States 1900-1939. U. S. Dept. Agr., Soil Cons. Ser. Miscl. Pub. **421**. 7 pp., 95 plates.

U. S. Bureau of Agr. Econ. & Tex. Agr. Expt. Sta. 1946. Agricultural production—Texas—1947. Tex. Agr. Expt. Sta., Bd. Mimeo., 65 pp.

U. S. Dept. Agr. 1938. Soils and men. U. S. D. A. Yrbk. Agr. 1938. 75th Cong., 2d Sess., House Doc. No. 398. U. S. Govt. Print. Office. Washington.
1941. Climate and man. U. S. D. A. Yrbk. Agr. 1941. 77th Cong., 1st Sess., House Doc. No. 27. U. S. Govt. Print. Office. Washington.
1942. Survey report on the Trinity River Watershed. 77th Cong., 2d Sess., House Doc. 708. U. S. Govt. Print. Office. Washington.

Warner, R. M. 1945. Relation of vegetative cover to the plant growth conditions of eroded soils. Iowa State Coll. Jour. Sci. **20**: 101-153.

Weaver, J. E., & F. E. Clements. 1938. Plant ecology. 2d ed. 601 pp. McGraw-Hill Book Co., New York.

Weaver, J. E., & W. W. Hansen. 1941. Native midwestern pastures—their origin, composition, and degeneration. Univ. Nebr. Conserv. & Surv. Div. Bul. **22**. 93 pp.

Williams, S. T., & B. D. Simison. 1937. Washington Irving on the prairie, or, a narrative of a tour of the southwest in the year 1832 by H. L. Ellsworth. 152 pp. Amer. Book Co., New York.

AN ECOLOGICAL STUDY OF SNAILS OF THE GENUS BUSYCON AT BEAUFORT, NORTH CAROLINA

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CONTENTS

AN ECOLOGICAL STUDY OF SNAILS OF THE GENUS BUSYCON AT BEAUFORT, NORTH CAROLINA

INTRODUCTION

Snails of the genus Busycon are among the commonest marine gastropods of the eastern coast of the United States. Mature individuals are larger than any other snails of the littoral region from Cape Cod to Cape Hatteras. Busycons because of their remarkable size and wide distribution are used as typical representatives of the prosobranch group of mollusks for classroom study (Drew 1936) and for research (Bergmann 1934, Redfield 1934, Wilhelmi 1944). Some unusual features that stimulate additional interest in this genus are the normal and common occurrence of both sinistral and dextral coiling of shells, smooth and hirsute periostraca, variability of spine length, brilliance of inner shell coloration, and finally the possibility of sexual dimorphism in size and shape of shells. A group with so many contrasting and varied characteristics provides excellent experimental material for zoologists.

It might be expected that the ecology of a group of animals of such distinction would have been thoroughly investigated, but this is not the case. The lack of ecological information may be correlated directely with the generally unrecognized commercial importance of these snails. Extensive ecological studies of single species, or genera, of mollusks are usually government sponsored projects concerned with animals of obvious economic value either as food, or as destroyers of food. Two investigations of this type that have been undertaken at Beaufort, North Carolina, are the work of Gutsell (1930) on the bay-scallop, an edible pelecypod, and Federighi's (1931) study of the oyster drill, a predacious snail. Busycons are of some economic significance. The muscular feet of these snails can be converted into chowder and "steaks"; the shells are widely used as ornaments. Finally Busycons have a nuisance value since they prey upon edible mollusks and destroy bait.

It is evident that there is need for basic ecological information of animals of such definite experimental and practical value as Busycons. The aim of the present study is to summarize ecological literature on the genus, Busycon, and to present the results of observations made on the species of this genus studied at Beaufort, N. C., during the summers of 1942, 1943, and 1944. The original work is primarily a population study with emphasis on seasonal and diurnal rhythms. Preliminary material is presented on growth, life history, consorts, food, and enemies. It was hoped that these ecological observations might contribute to the solution of the problem of species determination in the genus investigated.

The author is indebted to Dr. A. S. Pearse, who provided inspiration for the problem and guided its progress with kindly encouragement. Thanks are due to Dr. H. F. Prytherch, Director of the Beaufort Biological Laboratory of the United States Fish and Wildlife Service for the use of laboratory facilities during the summer of 1942. Welcome advice on mollusk problems has been given by Drs. W. J. Clench, H. van der Schale, J. P. E. Morrison, Burnett Smith, and Maxwell Smith. Without the ready cooperation of students and staff of the Duke University Marine Laboratory in the collection of specimens a study of this scope would have been almost impossible.

REVIEW OF LITERATURE

Long before man was concerned with such specialized branches of knowledge as ecology, or even conchology, mollusks were collected and propagated. Primitive peoples used these animals as food and their shells for utensils, ornaments, or money. Interest in these invertebrates is thus stimulated by their direct association with basic human needs. Oysters and their culture are perhaps the most thoroughly investigated subject in the entire field of marine invertebrate zoology. Mollusks are studied because of their cultural appeal both as objects of beauty and curiosities of nature. Poets have found inspiration in the intricate details of shell architecture. The variety of shapes and colors of molluscan shells arouses the collecting instinct in people of all ages. Epicures delight in the flavors of succulent species. A long and romantic history is associated with pearls, which are merely products of molluscan metabolism. Finally research on mollusks is sometimes undertaken in the interests of pure science when the goal is to discover basic facts of the behavior, structure, or life activities of these animals. The varied relationships of mollusks and man have led to the production of a voluminous literature, which is strangely lacking in detailed, or exact, information on the ecology of any species of only moderate economic importance.

The literature pertaining to the genus Busycon as it has been studied in the Beaufort region consists primarily of systematic lists of species with occasional notes of ecological interest. The most complete list of the varieties and species that might be expected in North Carolina is that of Johnson (1934) which gives the following six varieties:

1. ***Busycon carica carica*** Gmelin 1790
2. ***Busycon carica eliceans*** Montfort 1810
3. ***Busycon perversum perversum*** Linne 1758
4. ***Busycon perversum kieneri*** Philippi 1848
5. ***Busycon canaliculatum*** Linne 1758
6. ***Busycon pyrum*** Dillwyn 1817

Busycon carica carica, or *B. carica*, is reported in all accounts of Beaufort mollusks from Stimpson (1860) to Hackney (1944). This species, or variety, is characterized as either abundant, or common (Coues 1871, Osborn 1887, Jacot 1921, Pearse 1936, Pearse, *et al.* 1942). W. J. Clench, Burnett Smith, and Maxwell Smith consider *Busycon eliceans* a distinct species and not a variety of *B. carica* and for that reason the name *B. carica* is used throughout the remainder of the present paper.

No reports of *Busycon carica eliceans*, or *B. eliceans*, in the Beaufort region were found in any of the literature examined.

If *Busycon carica* and *B. eliceans* are considered as distinct species, it is then logical to consider *Busycon perversum* and *B. kieneri* as species and not as subspecies, or varieties. A recent article by Burnett Smith (1939) shows clearly that the name *B. perversum* is incorrect if applied to the slender sinistral Busycons of the type found at Beaufort. The name *B. perversum* should be applied only to the robust form described as a distinct species, *B. kieneri*, by Philippi (Smith 1939). Smith further proposes that the name *B. contrarium* be used for slender sinistral Busycons previously known as *B. perversum*. Since this new terminology has been employed by both Perry (1940) and Hackney (1944), it seems advisable to adopt it for this paper.

Busycon contrarium (*B. perversum* of authors) is reported as either present, common, or occasional near Beaufort (Stimpson 1860, Coues 1871, Jacot 1921, Pearse 1936, Hackney 1944). Richards (1936) states that beach-worn shells of this species may be fossils and not of recent origin.

No record is known of the occurrence of *Busycon perversum* (*B. kieneri* of authors) in the Beaufort region.

Busycon canaliculatum is characterized as either scarce, occasional, present, or common, depending on the season and habitat from which collections were made (Stimpson 1860, Coues 1871, Osborn 1887, Hackney 1944).

Busycon pyrum occurs, in three lists of mollusks of the Beaufort region, but these records appear to be based on dead shells and not on living specimens (Stimpson 1860, Coues 1871, Hackney 1944).

Of the six species of Busycons that might be expected in the Beaufort region there are three, *B. eliceans*, *B. perversum*, and *B. pyrum*, which have not yet been reported living in the littoral region. The remaining three species, *B. carica*, *B. contrarium*, and *B. canaliculatum* are known as common, or occasional, inhabitants of the littoral zone in a variety of habitats in the vicinity of Beaufort.

THE BEAUFORT REGION AND COLLECTING AREAS

Beaufort, North Carolina, is ideally located for marine biological research since it is situated in the mid-region of the Atlantic Coast of the United States in an area of transition between northern and southern faunae. The district is particularly suitable for ecological studies because there are several different types of habitats which are relatively undisturbed by man and his activities. The Duke University Marine Laboratory and the Laboratory of the United States Fish and Wildlife Service are both located on Piver's Island in Beaufort Harbor, which lies at one of the southern outlets of Pamlico Sound where it joins Bogue Sound. Beaufort Inlet is about 75 miles southwest of Cape Hatteras, a location frequently cited as the northern, or southern, limit of distribution for species of mollusks.

Observations were made at six stations indicated by Numbers I-VI on the large scale sketch map in Figure 1. A brief description of each of these stations is as follows:

I. Town Marsh on a sand and shell beach with almost no slope, but near a deep channel and a small oyster bed.

II. West shore of Piver's Island on a muddy bottom close to deeper water; Area and Atrina are characteristic pelecypods of this station.

III. Town Marsh on a muddy sand beach close to a permanent deep channel; oysters and Tagelus are typical pelecypods of region.

IIIA. Town Marsh close to Station III, but nearer oyster beds; bottom muddier than at Station III.

IIIB. Town Marsh east of Station III with bottom of sand, mud, clay, and shells in a shallow channel that was present even during the lowest tides. Current swift at changes of tide. Tagelus was quite common.

IV. Bird Shoal below low tide mark in a shallow tide pool that remains even during extreme low tides. Bottom here was a muddy sand.

V. Town Marsh east of Station IIIB on a muddy sand flat usually covered with six or eight inches of water during average low tides, but entirely exposed at spring tides. Tagelus, Venus, and an occasional Macrocallista are characteristic of the region.

VI. In transition region between Town Marsh and Bird Shoal with a sandy bottom with a small amount of mud. Venus is the characteristic clam of the station. The water depth at average low tide was about four to six inches.

The relationship between these stations and the tide levels is as follows: Station I was between tide marks; III, IIIA, V, and VI were below the low tide level during usual tides, but they were exposed at spring tides; II, IIIB, and IV were under water all of the time. The stations described were used primarily as places to which marked specimens were returned.

Some of the more significant characteristics of the Beaufort harbor that may have influenced some of the observations and results obtained during the present study are described as follows:

Bottom. Beaufort Harbor is shallow and shoal obstructed with a bottom that shows considerable

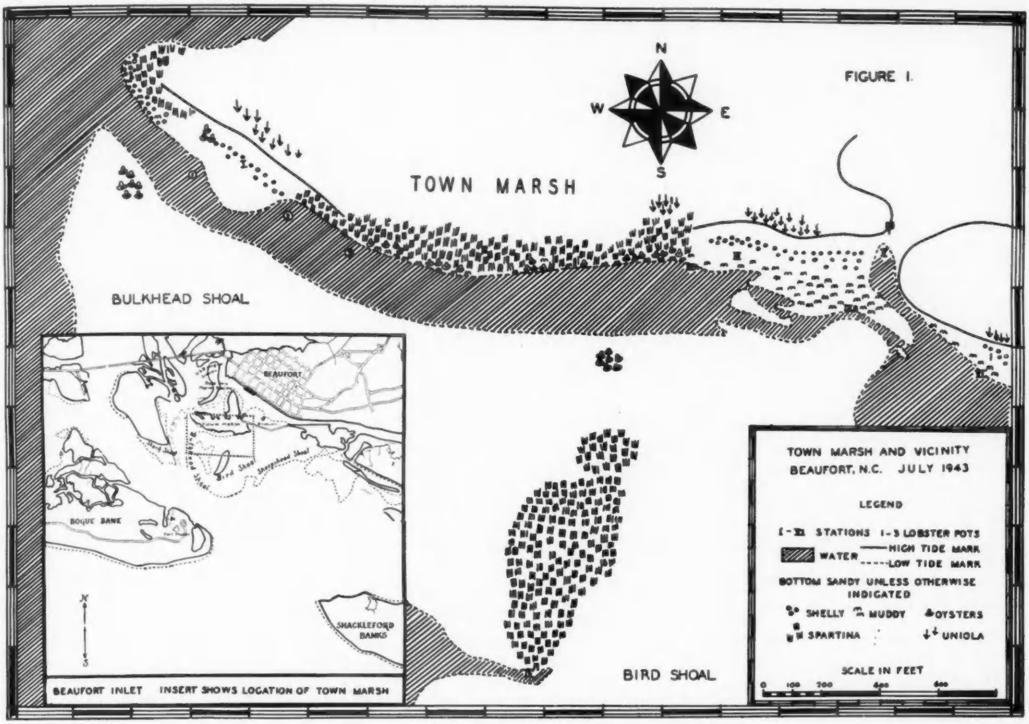


FIG. 1. Sketch map of a portion of Town Marsh showing the position of the stations to which specimens were returned. The position of the area in the sketch map in relation to other places of interest in the Beaufort harbor is indicated in the map in the lower left corner.

variation from shell and sand to mud and clay. In the areas observed most carefully the characteristic bottom was a mud-sand mixture.

Depth of Water. Regular observations were made at stations on Town Marsh and Bird Shoal that were under two to five feet of water at high tides and exposed, or covered by not more than two feet of water, during low tides. The Piver's Island Station (II) was located on flats that were covered by at least 18 inches of water at low tides. A few collections with trawl and dredge were made in water over six feet deep in the open ocean off Bogue Bank.

Currents, Wave Action, and Turbidity. Collections were made for the most part on Town Marsh and Bird Shoal where currents were moderate except for a short while just before and after low tides when occasionally rather strong currents were observed. Wave action was negligible on the sheltered flats within the Beaufort Harbor except during severe storms and very strong winds. Turbidity was usually not excessive. On Town Marsh specimens were easily seen in two feet of water under ordinary circumstances. On Bird Shoal with its sand bottom specimens were visible under three feet of water. The turbidity varied considerably with the direction of winds, presence of silt following severe rain storms, or local dredging operations. During March 1943 the water was so turbid that white collecting shoes could not be seen under six inches of water.

Wind. The prevailing winds throughout most of the year are from the southwest. Occasional storms come from the northeast. During the entire year of observations from June 1942 to June 1943 only one trip in the latter part of January 1943 was made with a strong northeast blow. All other trips were made with the wind from the west or southwest. The presence of even a slight wind might influence the number of specimens obtained by causing surface ripples that decrease visibility in shallow water.

Salinity. Gutsell (1930) concluded from his study of the scallop that adult animals may die several weeks, or even months, after a sudden decrease in salinity. With such long periods between the time of change in salinity and the response on the part of the animal it seemed impractical to make salinity determinations at the time of collection of specimens when the significant changes might well have occurred in the period between observations. The stations visited were in regions where the salinity is usually about thirty parts per mille. Gutsell (1930) recorded the monthly extremes of salinities for five years at Piver's Island. The greatest salinity observed was thirty-eight and the lowest was six parts per mille. This maximum value was observed five times in July

and August, but the minimum value was observed only once. The second lowest salinity recorded was that of fourteen parts per mille. Such a value was observed twice during the period of study. The salinities at Piver's Island might be somewhat lower than those of the water on Town Marsh-Bird Shoal flats where the water is shallower and nearer to the open ocean. Pearse, Humm, and Wharton (1942) noted an average salinity of thirty-four parts per mille on Bird Shoal during the summer of 1939.

Temperature. No attempt was made to record the daily fluctuations in temperature at the different stations, but readings of air, water, and sand temperatures were made during each collecting trip. An examination of the data of Gutsell (1930) and McDougall (1943) on water temperatures throughout the year at Piver's Island indicate that the months may be grouped into similar pairs. The months of a pair show greater similarity in maxima, minima, and means than the months of different pairs.

TABLE 1. Water temperatures in degrees Centigrade at Piver's Island 1924-1928 and 1941-1942. Months paired for similar temperature characteristics.

Month	Maxima 1924-1928 (Gutsell 1930)	Minima 1924-1928 (Gutsell 1930)	Means 1941-1942 (McDougall 1943)
January	14	5	7
February	16	9	6
March	18	8	8
December	18	6	11
April	22	14	15
November	22	11	15
May	26	19	20
October	28	15	22
June	30	23	25
September	30	23	26
July	31	25	28
August	30	25	27

The water temperatures observed during collecting trips were in all cases within the ranges for maxima and minima reported for Piver's Island by McDougall (1943) except for four instances when the temperatures were greater than previously reported maxima. Observed temperatures exceeded 1941-1942 values by the following amounts: 1.5° C. in November 1942, 10° C. in March 1943, 7.5° C. in May 1943, and 6° C. in June 1943. It is to be expected that the temperature of the shallow water over the sand and mud flats of Town Marsh and Bird Shoal might easily exceed that of the deeper water in the channel near Piver's Island.

METHODS AND APPARATUS

The principal method of this study was the observation of specimens under as many different natural conditions as possible. Some animals were collected and studied in the laboratory. The majority of these specimens were marked, measured, and returned to field stations for further study.

Collecting Techniques. The usual procedure was to walk in a definite route for a given length of time and collect as many specimens as possible. The majority of the animals obtained by this method were under eight to twelve inches of water crawling along the bottom apparently in search of food, or a mate. In some cases the tip of a shell siphon, or a shoulder spine, protruded from the shallow water, or from exposed sand. The partly buried individuals were usually feeding, copulating, or in ovoposition. When no specimens were observed, or collected, in the usual sites additional regions were explored. A qualitative, or random, method was necessary because very little information was available on the habits and preferred habitats of Busycons. It was found to be impossible to predict an area suitable for quantitative studies.

Specimens were sought by digging through sand exposed at low tide with a spade, or fork. This method was quite unsatisfactory; only a few specimens were obtained and these were usually damaged by the implements used.

Both dredging and trawling were found to be unsatisfactory as methods of collecting. The number of specimens was quite small and very unpredictable. The most productive dredging and trawling trip was one off Fort Macon on July 1, 1942. At this time sixteen specimens were obtained during a four-hour trip. With the previously described walking and pick up method it was possible to collect as many as 210 specimens in a two and one half hour trip of two people to Town Marsh.

Occasional references may be found to the use of baited traps for obtaining living specimens of mollusks in deep water (Perry 1940, Dakin 1912). Near Woods Hole in Buzzards Bay specimens of *Busycon carica* and *B. canaliculatum* are caught in lobster pots in significant numbers (Sumner, Osburn, Cole 1913). Three lobster pots of the Woods Hole type were set out in the channel south of Town Marsh near Station I in the positions indicated by the numbers 1, 2, and 3 on Figure 1. The traps were excellent for catching large numbers of the common blue crab (*Callinectes sapidus* Rathbun), but no Busycons were ever obtained in this manner. One factor that may have contributed to the failure of this method was the presence of so many blue crabs. The crabs could easily swim up to the trap, enter it and destroy the bait long before the slowly moving snails could move over the somewhat unstable sandy bottom to the proper place.

Collecting Equipment. A heavy cotton, or burlap, feed bag of the hundred pound size was found to be the most satisfactory container for transporting specimens across Town Marsh to and from collecting stations and row boat.

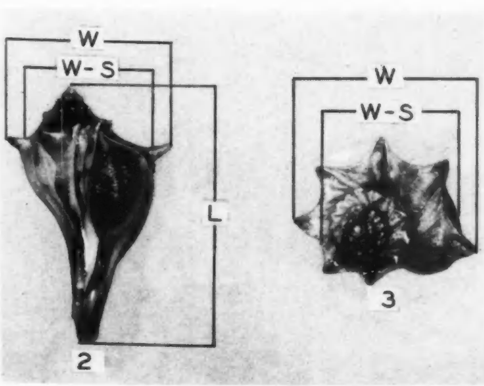
Identification of Specimens. Several methods of marking shells of specimens for identification of individuals were tried. A red plastic paint developed for the marking of sea turtles was found to be very

satisfactory for laboratory use. In the field exact identification of specimens marked with paint was impossible after only three days.

Numbered aluminum tags sold by the General Biological Supply House for use with small mammals, such as laboratory rats, were the most satisfactory type of marker used. Even after four years immersion in sea water recovered tags were still legible and showed no evidence of corrosion. These markers were easily and quickly applied; a hole was bored through the shell with a small electric hand drill. The tag was inserted in the opening and its tabs bent back flush with the inner surface of the shell. The ends of the tag inside of the shell were soon (in one case within three weeks) covered by newly formed shell so that after the tag had been in place for about one month it could not be removed without breaking the shell. Metal markers of this type were most satisfactory for the majority of specimens, but with shells less than six centimeters in length the drilling process occasionally broke the shell so that the tag could not be fixed in place. Some of the extremely large shells found were too thick for the tags.

An alternative method that was used on small shells and those too thick for application of metal numbers was to carve numbers directly on the surface of the shell with a small nine millimeter saw blade driven by an electric motor (a Craftsman Junior Motor Tool by Sears, Roebuck). The most convenient region of the shell for marking is the surface just below the shoulder (Figs. 5, 7, 30, and 53); for long time growth experiments if the shell is large enough it is preferable to mark the region between the suture and the shoulder as this area will not be covered by later growth of the shell.

Measurement of Specimens. All shells less than thirteen centimeters in length were measured with a steel vernier caliper to the nearest tenth of a millimeter. For dimensions greater than thirteen centimeters a wooden ruler was used. The length and width were measured as shown in Figure 2. It was



FIGS. 2 and 3. A specimen of *Busycon carica* with large spines. Fig. 2. Apertural view to show measurements made. L = length; W = width with spines; W-S = width without spines. Fig. 3. Apical view. W = width with spines; W-S = width without spines.

soon realized that the width measurement (w) was influenced greatly by the length of the shoulder spines. These spines vary considerably in different individuals of the same size and at different times in the development of a single individual. In an attempt to determine width independently of spine length a measurement (w-s) was made (Figs. 2 and 3). The degree of accuracy of the measurements is indicated in Table 2.

TABLE 2. Variations in repeated measurements of two Busycon shells.

SMALL SHELL				LARGE SHELL		
length	width	width−s		length	width	width−s
126.2	71.3	61.3		210	123	107
126.4	71.2	61.5		210	125	108
126.4	71.5	61.0		211	126	107
126.3	71.0	61.0		212	128	110
125.9	71.4	62.6		210	126	108
126.2	71.3	61.5	mean	211	126	108
±0.3	±0.3	±1.1	range	±1	±3	±2

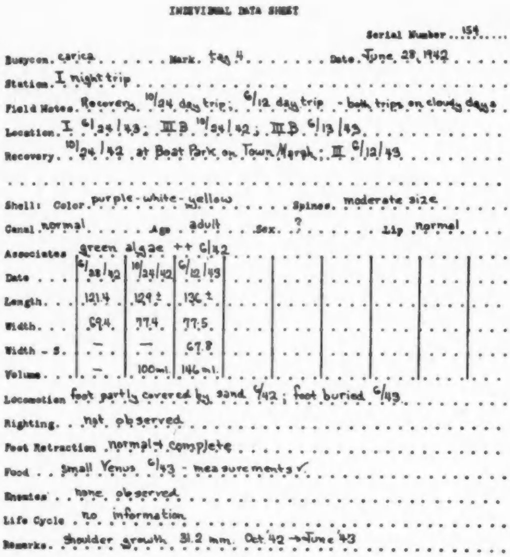
Under experimental conditions a greater degree of variation in measurements was obtained. Successive measurements were made several weeks, or months, apart and the shells might easily have been broken, or become worn, in the intervening time.

The volume of specimens was estimated by measuring the amount of water displaced when individuals were placed in graduated containers partially filled with sea water.

Preparation of Radulae. The method used was a modification of one suggested by Dr. Morrison of the National Museum. The shell was cracked off the specimen with a heavy hammer. The proboscis was dissected out and the radula was freed from most of the attached muscles. The radula was then left in a saturated solution of sodium hydroxide for several hours to macerate any remaining tissues. After the radula was washed well with water it was then transferred to a staining solution. The stain used was a mixture of equal parts of 1% aqueous crystal violet and .3% aqueous basic fuchsin. The radula was stained for one hour and then rinsed again in water and transferred to 50% ethylene glycol monoethyl ether for three hours. After thirty minutes each in two stoppered bottles of 100% ethylene glycol monoethyl ether the radula was mounted in hot balsam after clearing for thirty minutes in xylene.

Records. For each collecting trip notes were taken on conditions at the stations visited. Some of the factors observed were time of low tide, time of beginning and end of trip, route taken, strength and direction of wind, general weather conditions, depth, turbidity, and presence of surface ripples on water, temperature of air, water, and sand and also the activity of other animals in the areas observed.

An individual data sheet was compiled for each specimen. The form used is shown in Figure 4.



INDIVIDUAL DATA SHEET

Serial Number 154

Busycon. carica Mark. tag 4 Date. June 28, 1942

Station. I night trip

Field Notes. Recovery 10/24 day trip; 6/12 day trip - both trips on cloudy days

Location. I 6/28/42; III B 10/24/42; III B 6/13/43

Recovery. 10/24/42 at Boat Park on Town Marsh; III 6/12/43

Shell: Color. purple-white-yellow Spines. moderate size

Canal. normal Age. adult Sex. ? Lip. normal

Associates green algae ++ 6/42

Date	6/28/42	10/24/42	6/12/43					
Length	121.4	129 ±	136 ±					
Width	69.4	77.4	77.5					
Width - S.	—	—	67.8					
Volume	—	100ml.	146 ml.					

Locomotion foot partly covered by sand 6/42; foot buried 6/43

Righting. not observed

Foot Retraction normal → complete

Food small Venus 6/43 - measurements ✓

Enemies none observed

Life Cycle no information

Remarks. Shoulder growth 31.2 mm. Oct '42 → June '43

FIG. 4. A data sheet was completed for each specimen that was collected.

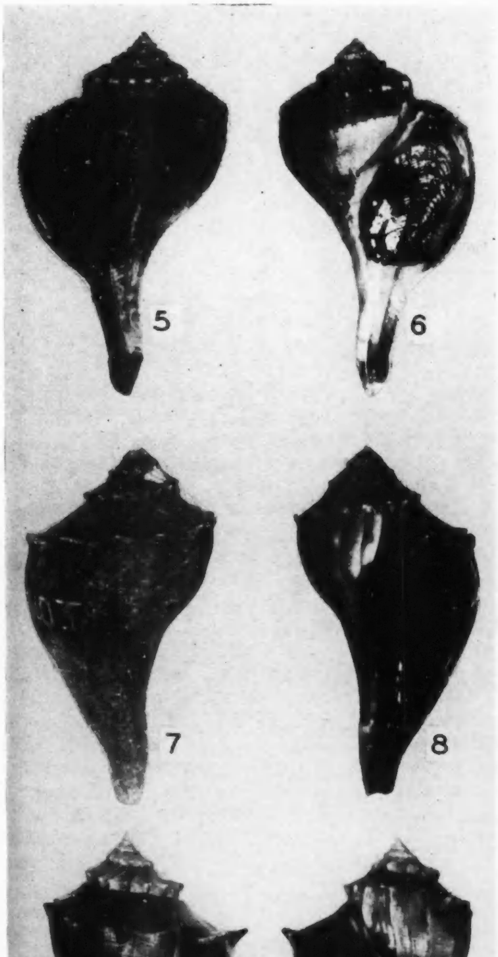
OBSERVATIONS ON ANATOMICAL CHARACTERISTICS OF BUSYCONS

Differences in behavior and ecological relationships may often be correlated with dissimilarities in the structure of animals. It seems appropriate for that reason to consider briefly some of the more obvious anatomical differences in the species of Busycon studied at Beaufort.

SHELL

Shape. A comparison of the shape of the shells of typical specimens of *Busycon carica*, *B. contrarium*, and *B. canaliculatum* is illustrated in Figures 5-10. It may be observed that the body whorl in *B. canaliculatum* is more globular than in either *B. carica*, or *B. contrarium*. The apical angle tends to be more acute in both *B. carica* and *B. contrarium* than it is in *B. canaliculatum*. The shell siphon in *B. canaliculatum* tends to be narrower and rather more sharply set off from the body whorl than it is in either *B. contrarium*, or *B. carica*. In comparing the proportion of body whorl and shell siphon in *B. carica* and *B. contrarium* there seems to be a longer siphon in *B. contrarium*. The shoulder angle in both *B. carica* and *B. contrarium* is more obtuse than it is in *B. canaliculatum*.

Thickness. The shell of *B. canaliculatum* is characteristically thinner than that of either *B. carica*, or *B. contrarium*. The thickness of the shell varies directly with the age and size of the specimens. Shells of *B. carica* and *B. contrarium* are of similar thickness if shells of similar length and development are compared. Mature shells of *B. canaliculatum* are usually about two millimeters in thickness; fully grown shells of *B. carica* and *B. contrarium* are usually about four millimeters in thickness. Measurements of shell thickness in several specimens of

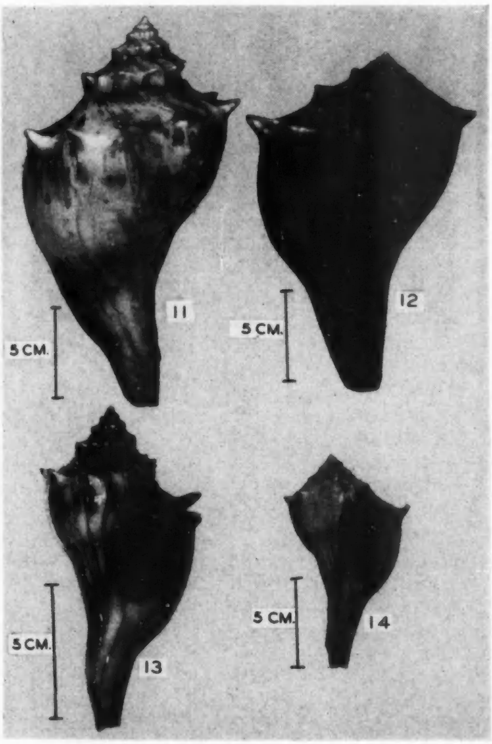


FIGS. 5-10. Typical specimens of three species of Busycons from Beaufort N. C. Figs. 5 and 6. *Busycon canaliculatum*. Figs 7 and 8. *Busycon carica*. Figs. 9 and 10. *Busycon contrarium*. Figs. 5, 7, 9. Nonapertural views. Figs. 6, 8, 10. Apertural views.

Busycon species are shown in Table 3.

Spire. The spire in Busycon shells is characteristically short. In *B. canaliculatum* it is turreted. It was observed that the tightness of coiling of shells of *B. carica* shows considerable variation. Extreme types of coiling are illustrated in Figures 11, 12, 13, 14. In some cases the latter whorls cover part of the spines of a previous whorl; in other cases the base of the shoulder is well below the spines. Such variation in coiling was not observed in specimens of either *B. contrarium* or *B. canaliculatum.*

Spinosity. In both *B. carica* and *B. contrarium* the shoulder of the whorls of the shell is accentuated by spines. In *B. canaliculatum,* however, spines are absent and the shoulder region of the shell is marked by tubercles. Spines are usually more conspicuous in *B. carica* than in *B. contrarium.* Even in a single species, *B. carica,* there is considerable variation in the number and size of spines present on the shoulder. A series of six individuals collected on one trip to stations IIIB, V, and VI presents a nice picture of the possible variation in spines (Figs. 15-32). It should be noted that the shell shown in Figures 30,



FIGS. 11-14. Four specimens of *Busycon carica* from Beaufort, N. C., with differences in tightness of coiling of the shell. Figs. 11 and 13. Loosely wound shells. Figs. 12 and 14. Tightly wound shells in which newer whorls actually cover part of the spines of previous whorls. Figs. 13 and 14. Apertural views. Figs. 11 and 12. Nonapertural views.

TABLE 3. Comparative shell thickness in three species of the genus Busycon.

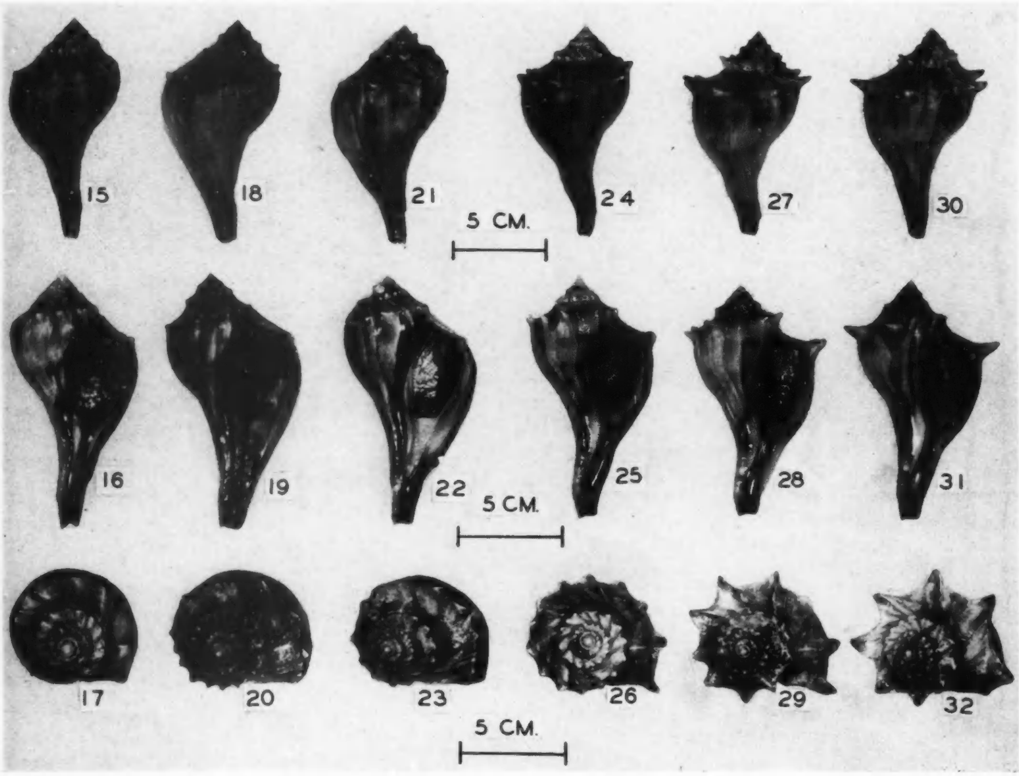
Species and Specimen Length	Shell Thickness
B. canaliculatum	
16 cm., old growth	1.6 mm.
15 cm., growing edge } same specimen	0.8 mm.
15 cm., old growth } same specimen	2.0 mm.
B. carica	
4.5 cm., old growth	0.4 mm.
16 cm., old growth	4.5 mm.
20.5 cm., growing edge } same specimen;	0.8 mm.
20.5 cm., old growth } mature not senile	4.6 mm.
20.5 cm., old growth—senile specimen	6.2 mm.*
B. contrarium	
5 cm., old growth	0.4 mm.
18.5 cm., growing edge } same specimen;	1.0 mm.
18.5 cm., old growth } mature not senile	4.7 mm.
18.5 cm., old growth—beachworn; fossil?	11.7 mm.*

*Thickest shells found during 1942-1943.
Measurements of shell thickness were made 2 cms. below shoulder and 2 cms. in from the outer lip of the specimen in the case of mature shells. In juvenile shells measurements were made in a comparable region.

31, 32 is quite similar in regard to spine number and size to shells of *B. eliceans* seen by the writer. The number and character of spines seems to show some variation with age; in both *B. carica* and *B. contrarium* spines are shorter and more numerous in young shells and larger and fewer in mature specimens. A gradual loss of spines with the onset of senility as described by Smith (1905) was observed in a few *Busycon carica* at Beaufort. Occasionally shells with recurved spines were observed (Figs. 33 and 34). Five specimens of *B. carica* were collected in which there was an extra row of spines midway between the suture and the edge of the shoulder. These extra, or abnormal, spines may be either more (Figs. 35, 36, and 37), or less (Figs. 38, 39, and 40) prominent than the normal shoulder spines. A fossil shell of *B. carica* and one of *B. contrarium,* both from North Carolina, and a recent *B. contrarium* from Florida with the extra row of spines are described by Smith (1943, 1944). Hackney (1944) collected at Piver's Island a single living specimen of *B. carica* with the double row of spines. At the present time a total of seven double spined individuals are known of *B. carica;* all of these are reported from North Carolina. Of the two double spined specimens of *B. contrarium* that are known, one is from North Carolina and one is from Florida. The double spined individuals are rather rare; it is estimated that there is about one in each three hundred of the Piver's Island-Town Marsh-Bird Shoal population of *B. carica.*

Sutures. The suture in *B. canaliculatum* is channeled, or canaliculate; it is this feature of the architecture of the shell that gives rise to the specific name. The sutures in both *B. carica* and *B. contrarium* are only moderately impressed.

Anterior Shell Siphon. The anterior shell siphon is that portion of the shell which covers the pallial



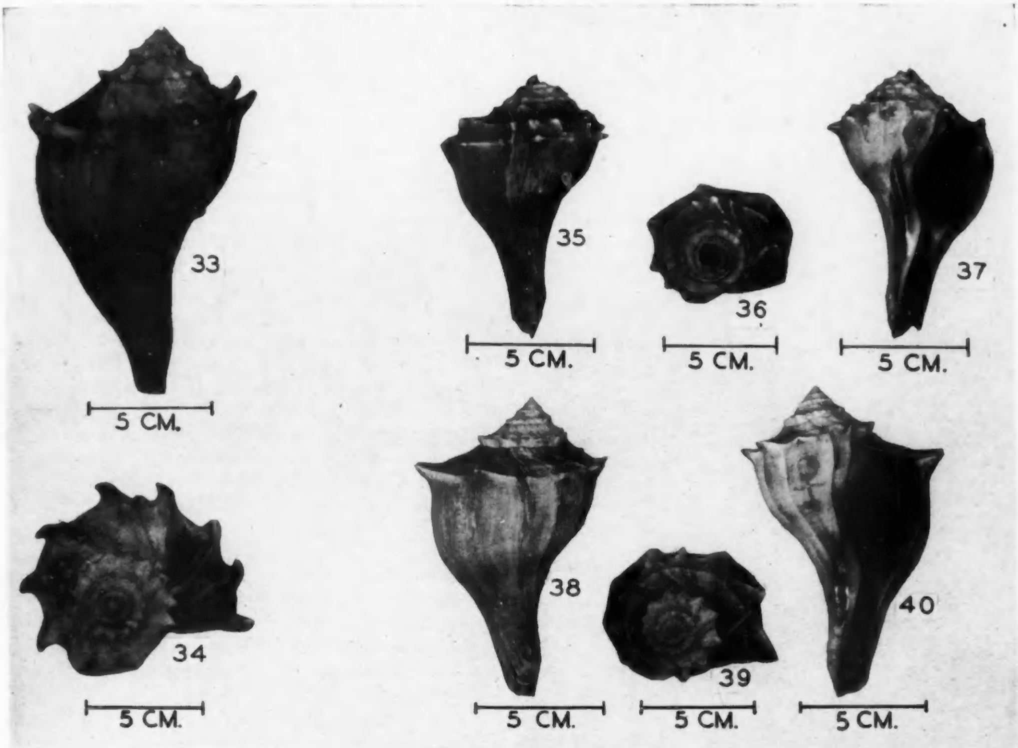
FIGS. 15-32. Variation in length of spines. A series of six specimens of *Busycon carica* obtained from a small area on Town Marsh near Station V that shows the extent of variability in spination from many small spines to a few large ones. Figs. 15, 18, 21, 24, 27, 30. Nonapertural views. Figs. 16, 19, 22, 25, 28, 31. Apertural views. Figs. 17, 20, 23, 26, 29, 32. Apical views. A single vertical row of figures consists of three views of the same specimen.

siphon. In *B. canaliculatum* the shell siphon is narrower and broader than it is in either *B. carica,* or *B. contrarium.* This part of the shell is often damaged by predators (Figs. 41, 42), but is easily repaired (Figs. 43, 44). It is unfortunate that such a vulnerable part of the shell is included in the length measurement. The anterior shell siphon, or canal, is said to be characteristic of carnivorous gastropods (Dakin 1912). Busycon, Fasciolaria, Eupleura, and Urosalpinx are some of the common genera of sea snails in the Beaufort region that have anterior shell siphons and have demonstrated their predatory habits in the field, or in the laboratory. In Polynices, however, there is no shell siphon, but the animal appears to be predatory. It feeds by boring a hole through the shell of its victim.

Sculpture. The sculpturing of the outer surface of the shell in both *B. carica* and *B. contrarium* is faint and variable, but both spiral and axial striations are present. Longitudinal lines of growth may be identified rather easily, but it is impossible to estimate the age of specimens by counting these lines. The surface markings of *B. canaliculatum* are more regular and prominent than in the other species. Quite often younger specimens of both *B. carica* and *B. contrarium* show elevated striae on the inner surface of the outer lip (Fig. 45); similar ridges have never been observed in *B. canaliculatum.*

Periostracum. One of the outstanding features of *B. canaliculatum* is a markedly hirsute epidermal layer, or periostracum, covering the shell. The periostraca of *B. carica* and *B. contrarium* is thin and not easily discernable. The appearance of the outer shell layer in *B. carica* and *B. canaliculatum* is shown in Figures 46 and 47.

Coloration. The outer surface of the shells of both mature and immature specimens of *B. canaliculatum* is a light tan, or beige, color. Adult shells of both *B. carica* and *B. contrarium* are definitely gray in color. The juvenile shells of these latter species show purple-brown stripes parallel to growth lines and contrasting markedly with a cream colored background. In many cases the shells of mature specimens are covered with a variety of attached organisms which effectively mask the color of the underlying shell.



FIGS. 33 and 34. Nonapertural and apical views of a specimen of *Busycon carica* with recurved spines.

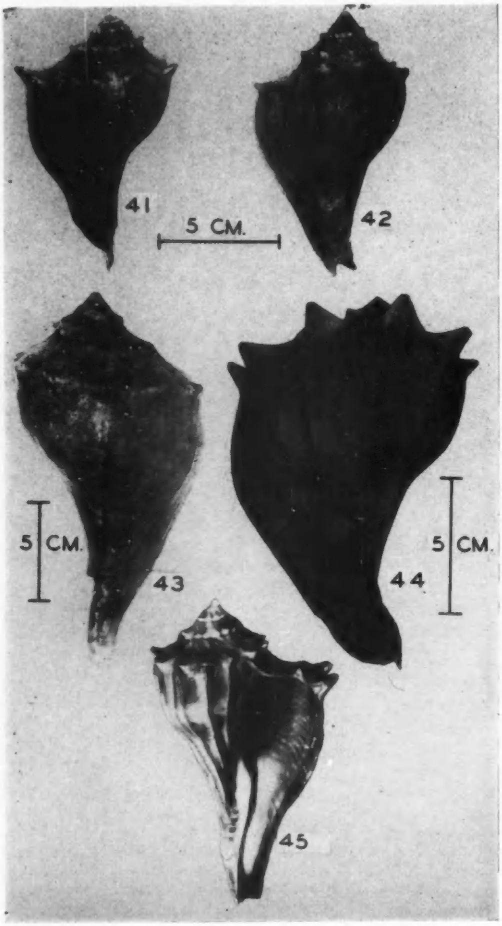
FIGS. 35, 36, and 37. Nonapertural, apical, and apertural views of an abnormal individual of *Busycon carica* with two rows of spines, one at the shoulder angle and a second between the shoulder and the suture. The abnormal spines are more pronounced than the normally place spines. This shell was dropped by a gull near the laboratory on a sidewalk. It has a broken apex.

FIGS. 38, 39, and 40. Nonapertural, apical, and apertural views of an abnormal specimen of *Busycon carica* with a ridge between the normal shoulder spines and the suture. This ridge is marked by very small spines.

The glazed inner surface of the shell mouth in *B. carica* is usually vividly colored in adult shells; the hue may vary from white, or pale yellow, to orange, or even a bright red. Older shells are often darker in color. In younger shells the mouth of the shell may be marked with white, yellow, or pale blue. The inner shell surface in *B. canaliculatum* is cream, yellow, or tan with pale purple markings. *B. contrarium* is always paler in coloration than either *B. carica* or *B. canaliculatum;* its columella is usually white while the inner surface of the outer lip of the shell is often marked with a pale blue.

Size. A comparison of the sizes of the three species of Busycon studied is presented in Table 4.

Only a few references were found that gave measurements of Busycon shells. Dall (1889) cites the maximum lengths for *B. canaliculatum,* 25.0 cms., *B. carica,* 20.0 cms., and *B. contrarium,* 37.5 cms. The Beaufort specimens of both *B. canaliculatum* and *B. contrarium* do not reach the maxima reported, but those of *B. carica* exceed the figure quoted by Dall. In fact in the group of one thousand specimens that were measured there were twenty individuals longer than the 20.0 centimeter maximum. There can be little doubt that the figure given by Dall is too small. Pratt (1935) gives the length and width of *B. carica* as 22 cms. and 11 cms., respectively, and the length of *B. canaliculatum* as 13 cms. These dimensions are well within the ranges determined for Beaufort species. Gould (1841) reports ordinary specimens from Massachusetts of *B. canaliculatum* are 15.24 cms. in length and 7.62 cms. in width with a maximum length for this species at 17.78 cms. Apparently the northern specimens of *B. canaliculatum* grow to a larger size than that characteristic of Beaufort. The figures cited by Gould (1841) for the size of an ordinary individual of *B. carica* are within the ranges determined for Beaufort specimens. The measurements given by Morse (1921) for *B. canaliculatum* from Woods Hole, Massachusetts, are within the ranges for Beaufort conchs. DeKay (1843) in his study of New York State mollusks gives 5.08-20.32 cms. as the size range for *B. carica* and 8.89-15.24 cms. as the range for *B. canaliculatum.* Richards (1938) in his study



FIGS. 41 and 42. Nonapertural views of two specimens of *Busycon carica* with tips of siphon canals broken by a stone crab, *Menippe mercenaria* (Say), in the laboratory. In Fig. 42 the tip of the black pallial siphon can be seen protruding beyond the end of the shell.
FIGS. 43 and 44. Nonapertural views of shells collected in the field showing damaged shells that have been repaired. Site of injury has been marked in black to show more clearly the extent of repair. Fig. 43. An old eroded shell of *Busycon contrarium*. An aluminum marking tag is fastened on the shell siphon near the tip.
FIG. 45. Apertural view of abnormal individual of *Busycon carica* with two spine rows. Striae may be seen between the operculum and the edge of the lip of the shell mouth on the inner surface of the lip.

of the marine mollusks of New Jersey gives 22.86 cms. as the maximum length for specimens of *B. carica*. DeKay, Gould, Morse, and Richards as might be expected gave measurements of shells in inches. These figures were converted to centimeters for purposes of comparison. Perry (1940) cites 30.0 cms. as the maximum length for *B. contrarium*.

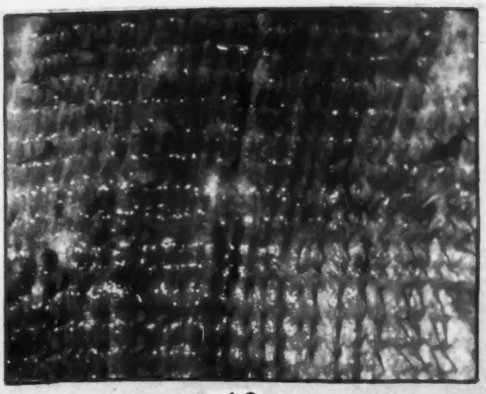
RADULA

The radula is a typically molluscan structure consisting of a flexible chitinous band covered with regular rows of teeth. Knowledge of the structure of the radula can be as useful to malacologists as information on dentition of animals is to mammalogists. The radular formula, the number of teeth in a single lateral row of the radula, is employed in classification of gastropods into families and even smaller groups. The number and character of radular teeth is an indication of the possible food habits of snails, in much the same way as the beaks of birds and teeth of mammals show the general types of food eaten.

The radular formula for Busycon is 1.1.1.; that is, in each row of teeth there is a single central tooth with a lateral tooth on either side. The central teeth are attached to the radular band with their anterior edges exactly transverse, while the lateral teeth are obliquely arranged and alternate with the central teeth. Stimpson (1865) in his study of the radulae of Busycons found that the central tooth of the radula in both *B. canaliculatum* and *B. pyrum* possesses only three denticles, in both *B. carica* and *B. contrarium* this same tooth has five denticles. The denticles of the lateral teeth seem somewhat more variable. There are four denticles on each lateral tooth in *B. pyrum*, five in *B. canaliculatum* and in a female *B. carica*, and six in a male *B. carica* and six in a male *B. contrarium* (Stimpson 1865). The results of the examination of eight radulae of specimens of Busycon obtained at Beaufort are shown in Table 5.

The radulae in Busycons are more variable than Stimpson's account indicates. In the smallest male specimen of *B. carica* one of the denticles of the central tooth was bifid throughout the entire length of the radula. A denticle of this sort has been described previously in *Nassarius reticulatus* (Pelseneer 1928). Considerable variation in the number of denticles in radular teeth has been reported by Dakin (1912) for *Buccinum undatum*, in which lateral teeth usually show four denticles and the central teeth from six to eight. Bateson in a study of twenty-seven radulae of this species found that the lateral teeth varied from three to five while those of the central teeth varied from five to nine. In some cases the opposite lateral teeth of a radula did not have the same number of denticles (Dakin 1912). A variation of this type was also observed in Busycon.

The total number of teeth in radulae of different snails is correlated with the type of food generally eaten by the animals. For *Buccinum undatum* the total number of teeth varies from 200 to 250 in a single radula (Cooke 1895). This species is known to be carnivorous. Its food consists of crabs, lobsters, and pelecypods (Dakin 1912). The total number of teeth per radula in Busycons varied from 270 to 400 for *B. carica*, 350 to 425 for *B. contrarium*, and 450 for *B. canaliculatum*. All three of these species of Busycon are carnivorous. Two marine snails known to be herbivores, Patella and *Littorina littora* have 2,200 and 3,500 teeth in their radulae (Cooke 1895).



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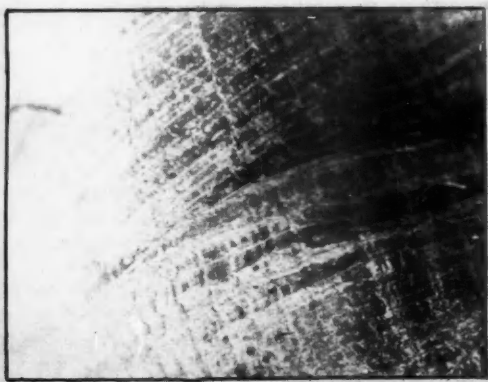

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FIG. 46. Surface view of Hirsute periostracum of *B. canaliculatum*. Fig. 47. Perisotracum of *B. carica* enlarged to the same magnification. Periostracum of *B. contrarium* is similar to that of *B. carica*.

TABLE 4. Summary of measurements of shells of species of Busycon collected at Beaufort, North Carolina, from June 9, 1942 to June 4, 1943.

	B. canaliculatum	*B. carica*	*B. contrarium*
number of specimens....	70	1,000	50
range in length (l)	7.2 - 16.3 cm.	2.7 - 24.0 cm.	5.2 - 26.0 cm.
mean length...........	12.4 cm.	9.0 cm.	14.4 cm.
number of specimens....	70	1,000	50
range in width (w)......	4.0 - 9.1 cm.	1.2 - 15.2 cm.	2.6 - 13.5 cm.
mean width............	6.4 cm.	5.0 cm.	7.9 cm.
number of specimens....	same as	319	34
range in width without..	(w)	1.2 - 12.5 cm.	2.5 - 10.6 cm.
spines (w-s) mean width - spines........	......	4.5 cm.	6.6 cm.
number of specimens....	70	319	34
range l/w-s	1.70 - 2.13 cm.	1.30 - 2.37 cm.	1.83 - 2.30
mean l/w-s	1.95 cm.	2.06	2.07
number of specimens....	64	826	49
range in volume........	23 - 260 ml.	1 ml. - 730 ml.	6 - 903 ml.
mean volume..........	113 ml.	73.6 ml.	176 ml.

TABLE 5. Measurements of Radulae from Beaufort Busycons.

Species Shell Length	RADULA		Rows of Teeth	NUMBER OF DENTICLES		
	Length	Width		Lateral	Central	Lateral
B. carica						
97 mm.......	38.7 mm.	2.8 mm.	90	5	5*	5
115 mm.......	53.5 mm.	2.4 mm.	113	6	5	5
215 mm.......	75.4 mm.	4.6 mm.	119	5	5	5
220 mm.......	76.4 mm.	4.6 mm.	133	5	6	5
B. carica (double spined shell)						
150 mm.......	50.7 mm.	2.8 mm.	113	5	5	5
B. canaliculatum						
142 mm.......	53.2 mm.	2.5 mm.	150	5	3	5
B. contrarium						
138 mm.......	64.2 mm.	3.8 mm.	137	5	4	5
177 mm.......	65.7 mm.	4.4 mm.	122	5	5	6

*One denticle was split at its tip and had two points instead of the usual one. All of the teeth in the radula show the split denticle in the same position in each tooth.

ECOLOGICAL OBSERVATIONS

Collections of Busycons were begun June 9, 1942 and continued until June 5, 1943. In this time one thousand specimens of *Busycon carica* were obtained and measured. The majority of these individuals collected were released for further study. During June, July, and August 1942 and June and July 1943 regular collecting trips were made at least once each week and occasionally as frequently as twice daily. From September 1942 through May 1943 at least two collecting trips, one during the day and the other at night, were made each month near the time of the full moon. A few sporadic observations were made during the summer of 1944. During the spring and summer of 1946 several collecting trips were undertaken.

POPULATIONS

Relative Numbers of Species of Busycon. In the time required to collect the first thousand specimens of *Busycon carica* only 29 individuals of *B. contrarium* and 61 of *B. canaliculatum* were obtained. The relative abundance of Busycons can be expressed by the ratio of 1 *(B. contrarium)* : 2 *(B. canaliculatum)* : 33 *(B. carica).* Coues (1871) suggested a 1 *(B. contrarium)* : 1 *(B. canaliculatum)* : 10 *(B. carica)* ratio, but his estimate seems to have been based on observations and not on an actual count. Even if this ratio proposed by Coues were correct, there are at least two reasons for an apparent change in numbers of the different species of Busycons in the Beaufort region. It is quite possible that in the seventy years between the work of Coues and the present

study there was sufficient change in environmental factors to cause an actual increase, or decrease, in the numbers of one, or more, species of Busycon so that a marked difference in ratios would obtain. It is also probable that the habitats observed by Coues were not identical with those emphasized in the present study.

In contrast to the situation at Beaufort, where *B. carica* is abundant and *B. canaliculatum* and *B. contrarium* are definitely less common, in the Woods Hole region *B. canaliculatum* is more common than *B. carica* and *B. contrarium* has never been reported. An approximation of the relative abundance of Busycons in the waters near Woods Hole can be made from the data of Sumner, Osburn, and Cole (1911). These investigators collected from both deep and shallow subtidal water shells and shell fragments of *B. canaliculatum* at 63 stations while similar traces of *B. carica* were obtained at only 20 stations. In this same study living specimens of *B. canaliculatum* were reported from 25 stations and *B. carica* at only 5. From these figures it could be concluded that in the Woods Hole region *B. canaliculatum* is obtained about five, or six, times as frequently as *B. carica.* The relative numbers of *B. canaliculatum* and *B. carica* collected from a variety of littoral habitats near Woods Hole indicate that *B. carica* is more common in the shallower water, but *B. canaliculatum* is still the predominant species by a ratio of approximately 3 to 1 (Allee 1923).

A report on the marine mollusks of Cape May County, New Jersey, by Wood and Wood (1927) indicates that all three species of *Busycon, carica, canaliculatum,* and *contrarium* are present in the region with *B. carica* about eight times as common as *B. canaliculatum.* No figures were cited for the relative frequency of *B. contrarium.* It was merely stated that a few were found.

Some conception of the character of the populations of the three species of Busycon commonly present at Beaufort may be obtained by a comparison of the frequency distribution of the lengths of shells of living specimens. A tabular summary of the shell lengths of Busycons is given in Table 6. For further comparison of the same data reference should be made to Figure 48.

Several differences in populations are shown by these curves. The curve for the *B. canaliculatum* population is the most symmetrical with only slight skew to the left. The regularity of this curve would perhaps indicate that *B. canaliculatum* is a more stable species and less inclined to show variation than either *B. carica,* or *B. contrarium.* The marked irregularities of the curve for the *B. contrarium* are in part due to the small size of the sample studied. The variation in length of specimens of *B. contrarium* is almost twice that of individuals of *B. canaliculatum* examined. The curve for the *B. carica* population shows marked asymmetry with a skew to the right. The shape of the curve is influenced by the large numbers of immature individuals that were obtained. The populations of both *B. contrarium* and *B. canaliculatum* are composed primarily of mature individuals.

TABLE 6. A comparison of the length of shells of living specimens of three species of Busycon. Collections made during 1942 and 1943.

Length of Shell in cms.	Number of Specimens Measured		
	B. canaliculatum	*B. carica*	*B. contrarium*
0 - 3.4	–	5	–
3.5 - 5.4	–	195	1
5.5 - 7.4	1	208	–
7.5 - 9.4	6	185	5
9.5 - 11.4	14	162	3
11.5 - 13.4	27	87	15
13.5 - 15.4	17	61	11
15.5 - 17.4	5	30	4
17.5 - 19.4	–	20	4
19.4 - 21.4	–	35	3
21.5 - 23.4	–	11	2
23.5 - 25.4	–	1	1
25.5 - 27.4	–	–	1
Totals	70	1,000	50

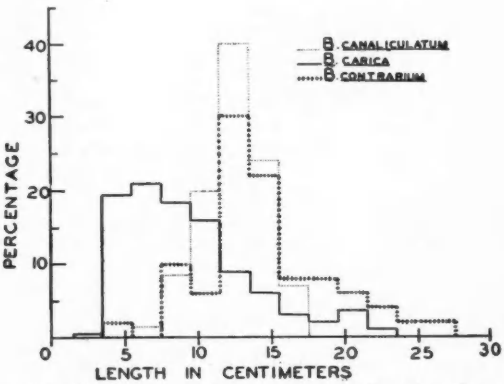


FIG. 48. Length of Busycon shells collected at Beaufort, N. C., from June 1942 to June 1943.

A comparison of the proportion of the shells in the three species of Busycon is presented in Figure 49. These curves seem to show that the proportion, that is the length divided by the width (w-s) of the shell, is more variable than is the length itself. The presence of the two, or three, peaks in each of the curves suggest that perhaps the ratio is different in immature, male, or female shells.

Recovery of Marked Specimens. Of the original group of one thousand specimens of *Busycon carica* that were collected, measured, and marked a total of 973 were released at the six stations shown in Figure 1. Of the 27 that were not released for further study there were nine that died in the laboratory tanks and 18 that were killed for specimens for anatomical work. A total of 87 individuals were recovered alive of the group of snails released. Of those recovered 88.5% were recovered only once; 9.2% were recovered twice; 2.3% were recovered three times. Fourteen shells were recovered in the field under a variety of

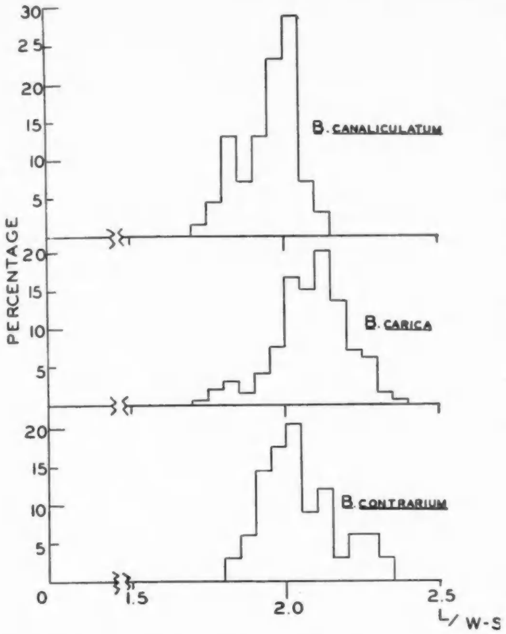


FIG. 49. Proportion (L/W-S) of Busycon shells collected at Beaufort, N. C., from June 1942 to June 1943.

circumstances. Four shells were found empty, or containing the remains of a dead animal. An additional five shells were obtained that were inhabited by hermit crabs. Two marked shells were recovered that were covered with salivary secretion of hungry larger conchs; it is presumed that the smaller specimens were eaten by their larger relatives. One broken shell was found inside of an old automobile tire that was serving as the "home" of a stone crab, *Menippe mercenaria* (Say). Another broken shell was recovered from a sidewalk near the laboratory where the gulls drop mollusks so that they can get at the edible portions of the animals. One specimen was recovered near Fort Macon, but the shell was broken and the animal killed by the human collector so the snail is considered as dead. Expressed in percentage the following recoveries were obtained: 8.9% recovered alive and 1.4% recovered dead which makes a total of 10.3% recovered.

Density of Population of Busycon carica. An estimate of the total number of individuals of *Busycon carica* present on the Bird Shoal-Town Marsh flats was made in the following manner. In this region 465 marked specimens were released. It is to be expected that some of these specimens released would have died, or been killed. According to the data already presented about one and a half percent of the entire number of individual snails released were known to have been killed, or died in a little more than a year. It is quite possible that an equal number of snails died that were not recovered. Four hundred and sixty-five less 3% would be 451. On July 1, 1943, a group of 38 specimens was obtained. Of this number five were marked. The five would represent about 1% of the number released in the area. If the total number that were collected also represented 1% of the total number of specimens in the region, the total population would be about 3,800. The area over which the collections were made was estimated to be about 300,000 square feet. This would allow for about 79 square feet for each snail, or one might expect to encounter a snail in each area 8.9 feet square.

Factors Influencing Recovery of Specimens. The number of specimens recovered varied somewhat from one station to another. At Stations II and VI only 3% of those released were recovered. At Station I, 6% were recovered while at Stations III, IV, and V the recoveries were close to 10% of the numbers that were released near those locations. At those stations located near deeper channels the percentage of recoveries was quite low. No satisfactory means was found for recovery of specimens from water deeper than three feet. Stations III and V were the most favorable for recovery of specimens. Both of these stations were located on, or near, rather extensive flats, which are almost entirely exposed during low tides. When collections were made on a falling tide while there was still one to two feet of water large numbers of specimens were obtained and the percentage of recoveries was high. It should be stated that the number of specimens recovered increased as the number of trips in a region was increased, or as the number of specimens released was increased.

RHYTHMS

Diurnal Rhythm. The activity of Busycons is influenced by innumerable factors so that it might be difficult to deterimne the critical factor, or factors, that might be operating at any one time. For greater accuracy it would be advisable to carry out daily observations for several years. However, observations throughout even a single year yield some suggestive results. It should be kept in mind that there is often some variation in numbers of specimens observed even under conditions that appear to be identical. During June and July, 1942 more active animals were observed at night than during the day at Stations I and III. In August of the same year the number of specimens collected during a rainy day was identical with the number collected the following night. A series of collections were made in a limited area on Town Marsh and Bird Shoal for several months. In all cases a day was chosen as near the time of full moon as possible and trips were made both day and night for about two hours just before the scheduled time of the low tides. As might be expected there was considerable variation in height of water, wind, strength of current, light and temperature. A summary of the results obtained is presented in Table 7.

In the habitat studied *B. contrarium* was never collected at night. It was obtained in water temperatures from 13° to 31.5° C. *B. canaliculatum* was not ob-

TABLE 7. Diurnal and seasonal variation in numbers of Busycons collected at Beaufort from September 1942 to June 1943.

Month	Time	*B. canaliculatum*	*B. carica*	*B. contrarium*
September....	Day	2	11	6
	Night	7	3	0
October......	Day	0	23	0
	Night	7	28	0
November....	Day	1	10	1
	Night	5	14	0
December....	Day	0	0	0
	Night	0	0	0
January......	Day	4	0	0
	Night	0	0	0
February.....	Day	4	1	0
	Night	0	0	0
March.......	Day	2	7	1
	Night	9	12	0
April.........	Day	2	17	4
	Night	2	18	0
May.........	Day	5	15	0
	Night	2	29	0
June.........	Day	2	61	2
	Night	0	52	0

served in December when the water temperatures were less than 8.5° C. In general more of these individuals were active at night. Specimens of this species were collected at water temperatures that varied from 8.5° C. to 31.5° C. The largest single collection of *B. canaliculatum* was made at a water temperature of 17.5° C. Individuals of the third species of Busycon were active both day and night. *B. carica* has been found moving about in water from 10.5° to 35° C. Large numbers of individuals were collected at water temperatures near, or just below 30° C. Small sized specimens of *B. carica* are more active during the day while more mature individuals are more abundant at night. In June the medium sized individuals were observed in approximately equal numbers during the day and night, but eighteen times more of the small specimens were out during the day and large individuals were three times as plentiful at night. Observations made of the activity of *B. carica* indicate that it varies with the season and with the size of the individual. It is possible that temperature, food, and enemies are some of the controlling factors in the establishment of rhythmic activity. Immature specimens of *B. carica* were active during the day in the summer; they were not observed except occasionally during the colder months. Young adults, or medium sized individuals seemed to be the most active. They were observed both night and day in approximately equal numbers except in very cold water.

The three species of Busycon present at Beaufort seem to show some evidence of daily rhythms. *B. contrarium* was observed to be diurnal in habits; *B. canaliculatum* is inclined to be more nearly nocturnal; *B. carica* is active both day and night. The number of *B. carica* recovered more than once was not sufficient to make any conclusions concerning the habits of individual specimens. One specimen that was collected three times was found active during the day twice and during the night only once. A second specimen that was taken three times was obtained twice during the night and once during the early morning. In the case of *B. carica* the number of animals active during the summer months varied with the amount of light, or temperature, in that large numbers were often collected on rainy days, in the early morning, or late evening, and on moonlight nights.

Tidal Rhythm. The exact relationship between the activity of Busycons and the state of the tide is difficult to demonstrate. Observations are more easily made at low tide. Changes in activity that are noticed may be the result of temperature or current differences and not dependent on the difference in amount of water present. Preliminary field observations indicated that more specimens were active two to three hours before the predicted time of low tide than at any other time during the day on both Town Marsh and Bird Shoal. Near Piver's Island, however, many specimens were collected an hour, or two, after the tide had started to rise. All attempts to obtain specimens during high tides were relatively unsuccessful. One factor that may have contributed to the lack of success is the decrease in visibility that accompanies the increase in depth of water. During the day specimens were usually collected under water that varies in depth from one half to four feet. At night snails are commonly found in water that is only a few inches deep; often parts of the shells of the snails seen would project above the surface of the water.

Seasonal Rhythm. As mentioned already in connection with diurnal rhythms the three species of Busycon characteristic of the Beaufort region show some seasonal variation in activity. In general, *B. carica*, is quite active throughout the year from March until December. During the winter months these snails are not very plentiful. *B. canaliculatum*, on the other hand, appears to be more active in the spring and fall when water temperatures would be cool, but not extremely cold. *B. contrarium*, which was never particularly common in the habitats studied, was obtained in largest numbers in April. A summary of the seasonal variation in numbers of Busycons collected is given in Table 8.

During the months of December, January, and February *B. carica* disappears almost completely from the sand and mud flats of Town Marsh and Bird Shoal. In the spring and fall, that is during the months of March, April, May, September, October, and November there were about half as many individuals of this species collected on a single trip as were found during the three summer months of June, July, and August. *B. carica* might be characterized

TABLE 8. Average number of specimens of Busycons collected per person per collecting trip on Town Marsh-Bird Shoal from August 1942 to June 1944.

Month	Number of Trips	*B. carica*	*B. canaliculatum*	*B. contrarium*
January	2	0	2	0
February	2	0.5	2	0
March	2	9.5	5.5	0.5
April	4	14.0	1	2.5
May	2	30.5	3.5	0.5
June	8	37.5	0.5	0.2
July	5	35.2	0.6	0.6
August	5	36.5	0	0
September	2	7.0	4.5	0
October	2	25.5	3.5	0
November	2	12.0	3.0	0.5
December	2	0	0	0

as the summer Busycon of the Beaufort region. *B. canaliculatum* is present in larger numbers in the spring and fall. It is occasionally found in the winter, but it is rarely found in the summer. *B. canaliculatum* might be considered as a cool weather conch. In the habitats studied *B. contrarium* is only an occasional visitor. Not enough individuals were observed to indicate the seasonal preferences of this species. Apparently *B. contrarium* was not well established on the Town Marsh and Bird Shoal flats.

A comparison of the numbers of specimens of different lengths (Fig. 50) that were collected during several months of the year indicates that there is a definite seasonal difference in activity in *Busycon carica*. To follow through the changes in a single year in January there were no active snails observed. In February the single active specimen was probably a mature male, or young female. By March there was an increase in number of active animals; the double peaked graph may indicate an increase in numbers of mature females, the longer individuals, and mature males, the moderate size animals. Beginning in April and continuing through May, June, July, August, and November there is a gradual increase and then a decline in the numbers of smaller, immature specimens.

MIGRATIONS

Observations made throughout the year indicate that Busycons show two distinct types of migration. One type of migration might be called horizontal and the other vertical. The horizontal migration from deep to shallow water is associated with reproduction and perhaps food supply. The vertical migration is also associated with food supply, tides, and the avoidance of predators and unfavorable environmental conditions, such as excessive heat, or light, and dehydration.

Early in the summer months large numbers of specimens were collected near Stations I and III. A little later many were obtained from the flat between Stations I and IV. Toward the end of the summer collections near Stations V and VI seemed to be larger than in either of the two previous places.

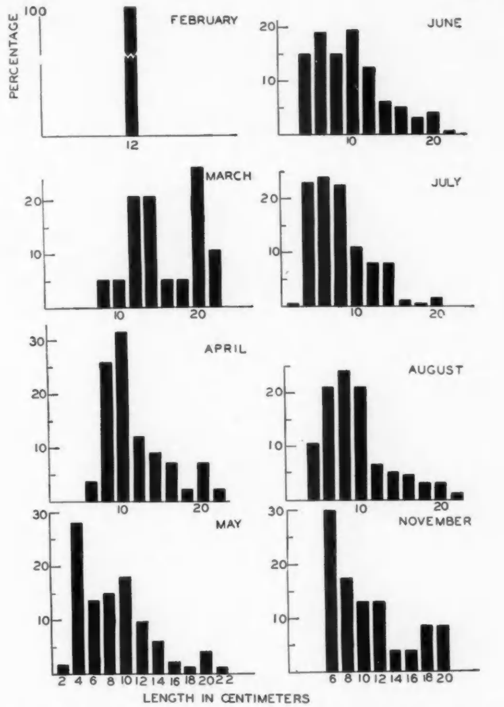


FIG. 50. Seasonal variation in shell length frequencies in *Busycon carica* population on Town Marsh-Bird Shoal, 1942-3.

More exact evidence of a horizontal type of migration was shown by the movements of marked specimens. Several specimens that were returned to Station I were recovered later between Stations I and III. Two specimens left at Station IV on the south side of a large Spartina bed on Bird Shoal were later recovered near Station III. One specimen returned to Station I on the southwest tip of Town Marsh was recovered four months later on a mud beach at the northern point of this marsh. The distance that had presumably been covered by this specimen was over 1,000 meters. This is perhaps possible if tidal currents and other factors are considered in addition to the locomotion of the snail itself.

Rate of Locomotion. Laboratory observations indicated that on a hard surface such as the bottom of a laboratory tank different specimens of *B. carica* moved at rates varying from 6 to 12 seconds per centimeter. In general small and medium size specimens moved faster than large ones. This would give an average rate of fifteen minutes per meter. One hundred meters would require one hour more than one day. In 18 days the 1,000 meter distance would be covered provided the snail crawled twenty-four hours a day. This amount of activity is quite unlikely. Field observations on movements of marked specimens showed that distances covered in a single

day varied from fifteen to forty meters. A great many animals did not move horizontally they merely buried themselves in the sand at the place where they were put. Of those that did move an average animal traversed about 18 meters in a day. At such a rate of speed the thousand meters would require about fifty-five and a half days.

Vertical Migration. In June 1943 a group of 33 specimens were released at Station I. After twenty-four hours only two specimens were found above the surface of the sand. Thirty-six hours later one specimen was still in sight and a second had come up out of the sand and was moving along the bottom. Similar results were obtained with other groups of snails. Almost immediately after they are returned to a station for release, the snails buried themselves in the sand. One, two, or three days later a few of the released animals might be observed moving about near the point of release. Quite a few recoveries were made about seven to eleven days after animals were released. Recovery of marked specimens often occurred one, or two months, or even a year or two following the time of return to the field. It seems likely that Busycons are active for a few hours a day for several days and then inactive for a longer time. The extent of the active and inactive periods could not be determined by the present study.

LIFE HISTORY

Sex Ratio. The sex of Busycons is determined by noting the presence, or absence, of a penis, a conspicuous structure located on the side of the head within the mantle cavity. This organ can be seen easily only when the animal is extended, or protruding part of the way out of its shell. To distinguish the sex of living specimens an animal is placed under water in such a position that the shell mouth is uppermost facing the observer. As the animal comes out of its shell and attempts to right itself the head and penis may be seen easily. Such a method is very time consuming because some animals will remain within their shells for an hour, or two, before attempting to right themselves. Drugs have been used to produce relaxation of muscles to permit forcible withdrawal of the animal so that its sex could be determined. Such a method was not used in the present study because there was the possibility that any drug used for this purpose might cause the death of the snail later and thus interfere with the population and migration studies. The sex ratios of several samples were determined and the results are shown in Table 9.

All of the specimens in the collections of July 1943 and April 1946 were killed in boiling water and the mantle cavity was opened so that the head could be examined carefully. These scattered observations indicate that there is some variation in the sex ratios in the different species of Busycon and even in the same species the ratio varies at different times of year. There appears to be no material on the sex ratios of Busycon in the literature studied. Some observations of Cole (1941) on the American Oyster drill, *Urosalpinx cinerea,* in England show even greater variability in sex ratios from 48.0% to 95% of the population studied were males. This author suggests the possibility of a sex change in part of the population. A sex change seems unlikely in Busycon, but the possibility should be kept in mind. The shell length for females varied from 3.5 to 21.6 cms. In males the shell length varied from 4.2 to 17.4 cms. Thus in the case of *Busycon carica* the majority of the males appear to be somewhat smaller in size than the females. In general the shells of the females appear to be longer and wider while the shells of the males are shorter and narrower in shape. It is expected that a statistical study of the proportions of the shell might show some sexual differences. It was also observed that the inner surface of the shells of male snails acquired a deep coloration while the shells were small in size. The deeper colored shells of female snails were usually the large, or very large shells. The possibility of sexual dimorphism in Busycons has not been suggested previously, but it has been found in *Buccinum undatum* (Morse 1876) and *Strombus pugilis* (Colton 1905).

TABLE 9. Sex ratios of Busycons collected on Town Marsh and Bird Shoal at Beaufort, North Carolina.

Date	Species	Males	Females	Undetermined
August 1942	*B. carica*	7	6	0
March 1943	*B. canaliculatum*	2	9	0
	B. carica	6	11	4
April 1943	*B. canaliculatum*	4	1	2
	B. carica	14	4	41
July 1943	*B. carica*	41	19	0
April 1946	*B. carica*	114	99	0

Breeding. Fertilization occurs internally in Busycons. On Town Marsh and Bird Shoal both *B. canaliculatum* and *B. carica* were observed copulating during March, August, and September. In the Beaufort region copulating snails have been observed as late as June. A pair of copulating individuals of *B. contrarium* were collected back of the mess hall on sand flats west of Piver's Island, but none were found in the Town Marsh-Bird Shoal area. During the breeding season it is quite common for two, three, or even four males to be found burried in the sand near a large female snail. At other times of year snails are usually collected singly.

Ovoposition and Fecundity. The eggs of Busycon are enclosed within capsules that are laid in long strings. The end of this string of capsules that is laid first is buried under the surface of the sand, or mud, about 10-20 centimeters. The buried end of the egg string produced by *B. canaliculatum* is often attached to a piece of shell, or some other hard surface. The strings produced by *B. carica* are not attached in this manner. The capsules produced by *B. carica* are known as the broad edge, or wide, type. This capsule consists of two plane surfaces about the

size of a quarter separated by a band. The effect is similar to that of a book in which the covers are separated by the pages. The type of capsule that is produced by *B. canaliculatum* is the narrow, or sharp, edge type in which one surface is joined by a second without any intervening band of material. In this sort of capsule there is one plane surface and one saucer shaped surface. In both types of egg strings the capsules are joined to one another by a strand of material similar to that from which the capsule itself is made. Opposite the region of attachment in each capsule there is a circular area at the edge which is of different appearance and apparently of different material than the remainder of the case. In mature egg strings this circular plug is missing; the hole that is left in the case serves as an exit through which the young snails can leave the capsule. In some of the older references to the egg strings of Busycon there was confusion of the types and it was stated that the narrow edge type was produced by *B. carica* (Coues 1871). This error has apparently been corrected in common reference books of recent years. Both Coues (1871) and Osburn (1887) reported that they had been unable to find the *B. canaliculatum* egg cases in the Beaufort region. No egg strings known to have been produced by *B. contrarium* were observed in the present study.

Recently produced egg strings were found on the Town Marsh-Bird Shoal flats for the first time during 1943 in the third week of May. A freshly laid string was found as late as June 24th in 1942, but the next year the last fresh strings were seen early in June. The fall period for production of egg strings was between the end of September and the middle of November in 1942. At this time two strings of *B. canaliculatum* and five of *B. carica* were found near the usual collecting places on Town Marsh and Bird Shoal. The following spring about thirty strings were laid in a comparable region.

Coues (1871) observe *B. carica* spawning in May at Beaufort. Smith, S. (1862) reported the presence of apparently freshly produced egg strings of both *B. carica* and *B. canaliculatum* in April and November on the Long Island shore. In the region of New Haven on the Connecticut coast ovicapsules of both *B. carica* and *B. canaliculatum* have been found in March and April. At Woods Hole freshly laid egg strings have been reported during the first two weeks in September when water temperatures were between 18 and 22° C. (Thompson 1890, Morse 1921). At the time of maximum egg string production in the spring of 1943 the water temperature was 20° C. while the temperature just below the surface of the sand was 21° C. *B. canaliculatum* egg strings were also reported from Narragansett Bay near Woods Hole, Mass., during the first week of June (Bumpus 1898).

The number of cases in each of twenty-four egg strings observed on the Town Marsh-Bird Shoal flats in the spring of 1943 at Beaufort varied from 9 to 156. In all cases only those capsules were counted that were above the surface of the sand. The mean number of cases per string was only 80. This number is lower than would be the case normally because many of the female animals were collected for food by a townsman while they were in the process of producing capsules. The freshly produced capsules may be seen for some distance on the flats at low tide and it is then easier to collect mature females than at any other time of year. The number of cases found in several strings observed is given in Table 10.

TABLE 10. Number of egg capsules above the surface of the sand in strings of the *B. carica* type observed at Beaufort, N. C., May 1943.

Number of Capsules	Number of Strings
0 - 19	4
20 - 39	3
40 - 59	3
60 - 79	2
80 - 99	3
100 - 119	3
120 - 139	3
140 - 159	3

Counts were made of the contents of three entire egg strings of the *B. carica* type. Two of these strings that were examined contained larval stages of developing snails; the third string was studied at the time of hatching of the young snails. The first string was 112.5 cms. long after it had been straightened out; in its natural coiled state it was only 105 cms. in length. Of the total 154 cases that made up this string there were 16 irregularly shaped, dull white cases that formed the anchor piece, or buried portion of the string. The second string of 139 cases had 19 in its anchor piece. This string was 83.8 cms. long straightened and 78.8 cms. coiled. Several different types of material were found within the cases of these two strings. In almost all of the intact cases there was an albuminous fluid in which segmented eggs, food eggs, and developing young in various stages were found. The total number of eggs in two strings examined are indicated in Table 11.

In one of the strings examined three cases contained well developed cultures of *Nitzschia closterium*

TABLE 11. Total number of eggs per capsule in two *B. carica* egg strings collected on Town Marsh, June 1942.

Number of Eggs per Capsule	String 1	String 2
0 - 9	29	24
10 - 19	4	9
20 - 29	8	21
30 - 39	17	40
40 - 49	36	37
50 - 59	28	7
60 - 69	24	1
80 - 89	6	0
90 - 99	2	0
Total	6,151	4,174
Mean number per case	41	34

Leidy, a diatom identified by H. J. Humm. Associated with the outer surface of the egg string such animals as barnacles, amphipods, and ascidians were found. A third string examined at the time of hatching contained 1,848 young snails all of which had dextral shells.

No references were found concerning the number of eggs in Busycon egg strings except for DeKay's rather amazing understatement that each case contained "one, or more young."

A large female conch, *B. carica*, that was producing an egg string was brought into the laboratory and placed in a large jar with sand and running sea water. Production of the egg string was continued at the rate of 6-7 cases in 12 hours. The following year a female was observed on Town Marsh that produced a string at the same rate. At such a rate even the longest string observed should require only about 5 or 6 days. A single unsigned report on *B. canaliculatum* in the Massachusetts region states that 8 days were required for the production of one string (anon. 1910).

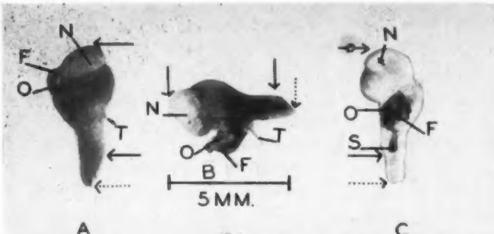
Growth

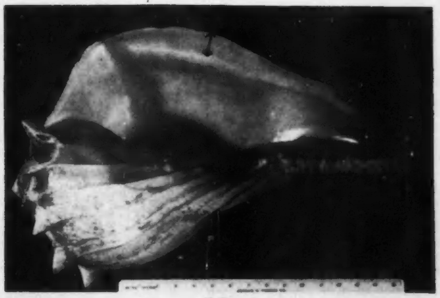
The entire group of specimens removed from one egg string at the time of hatching were kept in finger bowls and aquaria in the laboratory. A few of these specimens that lived to be 22 days old had added 1.5 mm. to the original shell length of 4 mm. The mortality rate of these specimens was extremely high, 97% died within three weeks. Some of the factors that may have contributed to the production of this high death rate were crowding, lack of sufficient food, or improper food, and lack of an adequate air supply. A small specimen of 22 days of age is shown in Figure 51.

All specimens recovered were remeasured to determine if growth had occurred during the period that they were in the field. Under natural conditions the shells of marine mollusks are subjected to considerable wear from the action of predators such as crabs and also from the effects of such physical environmental forces as currents and even waves. In many cases shells recovered after some time on the sand flats were actually smaller than when they were first measured.

As indicated in the section on Methods duplicate measurements of the same shell on the same day showed slight variation as shown in Table 2. A change of more than 0.3 mm. in either length, or width, of shells less than 13 cms. in length was considered to be an indication that growth had taken place. With specimens of more than 13 cms. length only changes of more than 1 mm. in length, and 3 mm. in width were considered significant. If changes were found in only one dimension it was still felt that perhaps growth had taken place.

Table 12 compares the numbers of specimens in which no apparent growth was observed with those which showed significant changes. This table shows that there is a minimum period during which no growth occurs. The number of small specimens that showed no change in size is rather large. Most specimens in which growth occurred were of medium size. A considerable number of large specimens are found in the group in which growth took place.

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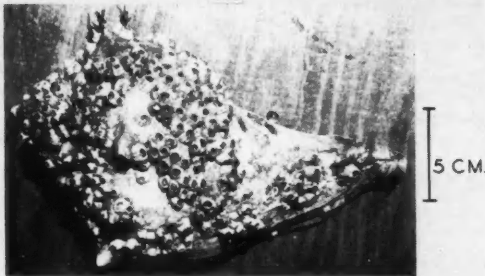

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FIG. 51. A 22 day old specimen of *Busycon carica*. A. Nonapertural view. B. Lateral view. C. Apertural view. Solid arrows indicate the original length of shell at the time of hatching. Dotted arrow indicates amount of growth in 22 days. N = shell nucleus: F = foot; T = tentacle; O = operculum; S = pallial siphon.

FIG. 52. A large specimen of *Busycon carica* with an area of new growth at edge of shell lip width marked by arrow.

FIG. 53. A large specimen of *Busycon carica* providing attachment for many barnacles and three tufts of red alga.

Usually the longer an animal remained in the field the greater was its change in size. As might be expected this condition does not hold without some exceptions as are seen in Table 13.

It has been suggested that each spine on the shoulder of the shell of a *Busycon carica* represents a year of growth. This suggestion is not confirmed by data collected on Beaufort specimens (Table 14).

It can be seen that the formation of a single spine requires a variable amount of time between 3 and 17

TABLE 12. Numbers of specimens of *Busycon carica* of different size groups in which no growth was apparent after different lengths of time in the field are listed under heading "NG." The number of specimens in which growth occurred are under G+.

Days between Measurements	Size Groups: Small less than 6.5 cms. NG	G+	Medium 6.6 to 13.0 cms. NG	G+	Large 13.1 to 18.0 cms. NG	G+	Very Large more than 18.1 cms. NG	G+	Totals NG	G+
1 - 10	3	—	8	—	4	—	—	—	15	0
11 - 20	6	—	3	—	2	—	—	—	11	0
21 - 30	3	—	—	—	1	—	1	—	5	0
31 - 90	1	—	6	7	—	1	—	—	7	8
91 - 180	—	—	—	2	1	1	—	—	1	3
181 - 360	—	3	1	8	1	4	1	—	3	15
361 - 540	—	1	1	9	—	1	—	—	1	11
541 - 630	—	—	—	—	—	2	—	—	0	2
631 - 720	—	1	—	4	1	—	—	2	1	7
721 - 810	—	—	1	1	—	—	—	—	1	1
over 811	—	—	—	1	—	1	—	—	0	2
TOTALS	13	5	20	31	10	10	2	2	45	48

TABLE 13. Relationship between days of growth and increase in length of shells of *Busycon carica* at Beaufort, North Carolina.

Increase in Length, mm.	Number of Specimens	Days for Growth: 30-180	181-360	361-540	541-720	721-900	over 900
0 - 1.0	15	4	6	1	3	—	1
1.1 - 2.0	2	1	1	—	—	—	—
2.1 - 4.0	8	3	3	2	—	—	—
4.1 - 8.0	11	3	2	4	2	—	—
8.1 - 16.0	7	—	3	2	2	—	—
16.1 - 32.0	3	—	—	1	1	1	—
32.1 - 64.0	3	—	—	—	2	—	1

TABLE 14. Rate of spine production in several specimens of *Busycon carica* observed at Beaufort, North Carolina.

Number of Spines Produced	Days Required: min.	max.	mean	Number of Specimens	Mean Number of Days Required for Formation of 1 Spine
1	403	680	501	6	501
1.5	...	706	...	1	471
2	454	677	566	2	283
3	381	398	389	2	126
4	380	412	396	2	94
5	677	691	684	2	137

months. A single specimen does not always produce spines at the same rate. One specimen, for example, produced five spines in 691 days, which is a calculated rate of 138 days for the formation of a single spine. During the next 706 days, however, this same specimen completed only one and one half spines. The rate of formation for a single spine in this case would be 471 days. It is then possible for five spines to be formed in less time than that required for the production of one and one half spines. A second specimen gave no evidence of spine production during a period of 205 days, but in the next 381 days three new spines appeared at a calculated rate of one for each 127 days. It can be seen that the rate of spine production is a variable process not only in different individuals, but also in the same individual at different ages and under various conditions.

Among mollusks the amount of growth and even ages of specimens are often estimated through examination of growth lines. A method of this type cannot be applied with any accuracy to Busycons. In the first place growth lines are difficult to distinguish in snails since new growth covers the old except for a very small area at the shoulder. Furthermore, examination of recovered marked specimens indicates that as many as three growth lines may be produced in a single year, but often no new growth occurs even after several years.

The rate of growth of different parts of snail shells is not identical. This difference in growth is a necessary condition for the production of the asymmetry that is so characteristic of gastropods. As might be expected the region of maximum growth is the edge of the outer lip of the shell. In some instances the shoulder shows the greatest growth rate, but in other cases a point in the mid-region of the lip (Fig. 52) exhibits the greatest change. The presence of shoulder spines makes the width measurement rather unreliable. The rates of growth of different parts of shells of *Busycon carica* are shown in Table 15.

Many of the specimens that were recovered and showed recent growth that could be confirmed by increases in shell dimensions had areas of uncompleted new growth at the outer edge of the shell mouth. These regions of new growth could be recognized by three characteristics: the outer surface was often slightly lighter in color than the remainder of the shell and not covered by the growth of algae, or other consortes; the inner surface was also a different color from that of the older shell; the entire area was much thinner than adjacent shell. These observations may indicate that the outer layer of new shell is laid down first and then additional layers are added to the inner surface as growth continues. Such observations are in accord with the more recent theories of shell formation among mollusks (Robertson 1941).

A comparison of the percentage increase in length calculated for a period of one hundred days for different size groups of *Busycon carica* reveals that growth is most rapid in medium size and possibly very large specimens. The rate of growth is less in large individuals and least in small specimens. In a group of five small (up to 65 mm.) specimens the maximum rate of growth was 1.9% increase in length per one hundred days; minimum was .3%; mean 1.46%. A larger number (29) of medium sized individuals showed a maximum of 9.8% with a minimum of .04% and a mean of 2.8%. Ten large sized snails showed a maximum of 6.4%, a minimum of 0.1%, and a mean of 2.12%. Only one very large individual was found that showed any change in length of shell.

TABLE 15. Increase in different dimensions of *Busycon carica* shells in which growth occurred. Small shells are those less than 65 mm. in length; medium = 66 to 130 mm.; large = 131 to 180 mm.; very large = over 181 mm.

Period of Growth	Days of Growth	Size Group	Increase in Size, mm.				
			Length	Width	Width-Spines	Shoulder	Middle Lip
June-July 1944	14	medium	2	0	6.6	–	17
May 1943-July 1944	417	medium	3	3.9	0	–	6
June 1942-June 1943	354	small	3.7	1.2	–	6.4	–
Aug. 1942-June 1944	680	very large	4	0	–	–	20
May 1943-June 1944	402	small	4.7	1.1	1.3	–	8
April 1943-June 1944	455	medium	5.6	6.8	2.7	–	13
Nov. 1942-June 1944	586	large	6	0	6.4	–	13
Aug. 1942-June 1943	296	large	6	10.6	–	20.4	19.6
Mar. 1943-June 1944	467	medium	6	3.8	4.8	–	23
Oct. 1942-June 1944	231	medium	7	0	–	31.2	–
Aug. 1942-June 1943	295	medium	8	11.2	–	18.9	20.9
Nov. 1942-June 1943	208	large	9	0	4.7	24.7	34.6
June 1943-July 1944	397	medium	9.9	5.3	–	–	31.0
Aug. 1942-June 1944	677	medium	11.0	3.8	–	–	30.0
July 1944-June 1946	706	large	13.0	6.0	1.8	–	28.7
June 1943-June 1944	380	medium	20.7	12.7	8.8	–	61.0
June 1913-June 1944	381	large	29.0	31.9	15.1	–	88.0
Aug. 1942-June 1944	677	medium	35.3	25.3	–	–	108.0
Aug. 1942-July 1944	691	medium	50.0	31.0	–	–	145.0

Its percentage increase in length for one hundred days was found to be 2.7%.

CONSORTES

In the littoral zone of the sea, where competition for survival is so keen, every available firm surface is used by sessile organisms as a place for attachment. Many different plants and animals are found adhering to Busycon shells. During June, July, and August of 1942 all specimens that were collected were examined briefly and the macroscopic organisms present on the shells were noted. The results of these observations appear in Table 16.

The green algae commonly found on Busycon shells were identified by H. J. Humm as *Ulvella lens* Crouan and *Enteromorpha linza* (Linnaeus). The Enteromorpha species determination was somewhat uncertain because of the limited material available, but in all probability the species is the one indicated. The only red alga was *Hypnea musciformis* (Wulfen); this consort was usually found attached to the tip of the shell siphon, or near the shell shoulder (Fig. 53). A single specimen of *B. carica* was found in which the shell was perforated by the boring sponge *Cliona* sp. Annelid tubes occurred on several shells; these tubes were often empty and identity of the original inhabitants could not be determined. One living tube dwelling annelid identified as *Sabellaria vulgaris* Verrill by Miss Martha Clark was rather

TABLE 16. Consortes of Busycon shells examined June-August 1942 at Beaufort, North Carolina. The percentages indicate the number of shells examined which supported consortes.

Co sort	*B. carica*	*B. contrarium*	*B. canaliculatum*
Green Algae	62.7 %	56.3%	0
Red Algae	1.3 %	0	0
Bryozoa	10.47%	0	0
Cliona	0.1 %	0	0
Annelid Tubes	4.5 %	0	13.3%
Anomia	0.0 %	6.3%	0
Crepidula	0.4 %	6.3%	0
Barnacles	13.2 %	25.0%	6.7%
No Consortes	29.5 %	37.5%	80.0%
Shells examined	687	16	15

common. A single specimen of *Anomia simplex* Orbigny was found on a *B. contrarium* shell. A few examples of *Crepidula fornicata* Linnaeus were observed on the shells of living animals. Several species of Crepidula and oyster spats are present in abundance on the deal shells of Busycons that are inhabited by hermit crabs. No identification of the barnacles found on Busycon shells was made for in most instances the specimens present were immature, or even dead. McDougall (1943) has stated that species determination of barnacles can be made only with mature individuals. R. C. Osburn identified two very common Bryozoan consortes as *Acanthodesia tenuis* (Desor) and *Alcyonidium polyoum* (Hassall).

FOOD AND FEEDING

Food preferences of Busycons were observed in the field and laboratory. Whenever animals were collected their feet and the sand immediately surrounding buried animals were examined for the presence of food organisms. A variety of pelecypods were kept in the laboratory tanks for food. Tanks were drained twice a day and any dying animals immediately removed; any pelecypod shells which remained after the Busycons had removed the contents for food were kept for measurement.

The favorite food of Busycons in the laboratory tanks was Tagelus. The popularity of this clam is perhaps influenced by three factors: it is unable to close its valves as tightly as some of the other types of clams; the shell is light and fragile; it was provided in greater numbers. Chione and Venus tie for second place as articles of Busycon diet.

A specimen of *B. canaliculatum* was found eating another snail of the genus Polinices. A large pail full of freshly collected specimens of *Busycon carica* was found to contain one small shell (56.3 mm. in length and 26.1 mm. wide) of *B. carica* that was covered with saliva and appeared to have been recently eaten. Gastropods do not seem to form a conspicuous part of the food of Busycons. A closely related snail, *Fasciolaria distans*, has frequently been observed eating smaller snails. Urosalpinx, Nassarius,

TABLE 17. Number and measurements in millimeters of shells of pelecypods eaten by Busycons in the field and laboratory at Beaufort, North Carolina.

Food Animal	Number Measured	length max.	length min.	height max.	height min.	width max.	width min.
Cardium sp.	1	18.2		17.5		12.5	
Chione cancellata	39	41.1	14.8	35.5	12.2	23.5	7.3
Divericella quadrisulcata	2	18.7	17.8	17.8	17.2	11.2	9.9
Dosinia discus	19	77.7	45.3	70.2	42.1	23.6	17.4
Ensis directus	1	†					
Macrocallista nimbosa	4	122.0	58.6	61.8	30.9	32.2	15.5
Modiolus demissus	10	79.2	34.1	33.7	16.4	24.6*	
Ostrea virginica	1	48.4		65.6		21.9	
Pecten irradians	5	48.3	26.5	46.4	26.4	23.1	14.6
Spisula solidissima	2	47.6	13.7	33.2	9.5	19.7	5.0
Tagelus gibbus	250	‡					
Venus mercenaria	27	90.2	11.6	77.8	10.1	54.7	5.6

†Shell broken; measurements not made.
*One valve broken; measurement impossible.
‡All sizes were eaten.

and Terebra have all been recovered in a partially eaten state from the foot of Fasciolarias, but not Busycons.

Not enough observations were made to indicate if there are any significant differences in food preferences among the different species of Busycons present at Beaufort. *B. canaliculatum* was found eating Polinices which was never known to have been eaten by either *B. carica* or *B. contrarium.* It is expected that the foods of the three species might be somewhat different because of differences in habitat and habits. An attempt was made to determine the amounts of food eaten by individuals of the different species of Busycon. Specimens of each of the three species of Busycon were placed in separate containers with weighed living Tagelus and Venus, but even after three weeks none of the food animals had been eaten so the experiment was discontinued.

It is quite possible that food preferences vary with age of animals. A few small specimens of *B. carica* have been collected with annelid tubes in their feet. These younger snails have also been observed to collect in areas where clumps of *Petaloproctus socialis* are found.

Busycons may also serve a function as scavengers. In the field they have been observed near dead Callinectes. In the laboratory they have eaten recently dead fish. In the Woods Hole region they are collected in lobster pots to which they have presumably been attracted by the bait.

Feeding. The process by which an animal obtains and ingests its food is of fundamental importance in determining its food, and even habits and habitats. Many of the earlier workers (Mendel and Bradley 1905, Herrick 1906, and Rogers 1920) suggested that Busycons obtained their food by boring a hole through the shell and sucking out the soft parts for food. Colton (1908) corrected this erroneous impression when he observed Busycons as they ate food in a laboratory tank. The manner of eating varies with the type of food eaten. A clam such as Mya, which is unable to close its shell completely and thus has its soft parts exposed, is held in the foot of a hungry Busycon and the soft flesh is ripped away in strips. This method of eating was employed by Beaufort Busycons for Tagelus and with dead fish. On the other hand, a different method of attack is used with pelecypods that have more solid shells which can be closed tightly. In eating an oyster, for example, *B. canaliculatum* was observed by Colton to wait until the shell opens slightly. The predatory Busycon inserts the edge of the outer lip of its own shell between the partially separated valves of the animal to be eaten. The valves of the prey are then forced apart sufficiently so that the proboscis of the Busycon can reach into the soft parts of the victim. This second method of approach is used by all three species of Beaufort Busycons for eating not only oysters, but also Doscinia, Macrocallista, and smaller Venus. A third and final method of penetration of pelecypod shells as described by Colton is carried out against the hard clam, Venus. In this case the prey is grasped in the foot muscle of a Busycon. The clam is held in such a position that when the columellar muscle of the snail is contracted the outer lip of the Busycon's shell is brought against the ventral edges of the clam's shell often with such force that either the clam shell, or the snail shell, or both are broken. This hammering of the edge of the clam shell is often repeated for some time; a rate of six times per minute was observed by Warren (1916). When the broken region of the shell of the prey is large enough the Busycon inserts the sharp shell lip between the valves and the Venus shell is wedged open. Both *Busycon carica* and *Busycon contrarium* were observed opening Venus shells by this method. None of the *B. canaliculata* observed were ever seen to use this method in Beaufort, but Warren (1916) has found this species eating Venus in the field. Clench (1939) observed a large *B. contrarium* open and eat a Venus. He believes that this shell chipping and prying method of eating is exceptional and not the usual practice. He suggests that the valves of pelecypod shells are pulled apart by suction of the foot. It is difficult to visualize such a process. In the first place the foot of most Busycons is too small to grasp large Venus shells and exert sufficient suction to be effective. It has been estimated that a force of 23 to 26 pounds is necessary to force open a Venus shell (Reese 1942). Four large Busycons which had their feet in firm contact with the bottom of a laboratory tank were easily detached when pulled by a spring scale, the hook of which was placed under the edge of the Busycon shell. The scale indicated that a pull of 4 to 6 pounds was all that was needed to remove snails from the bottom of the tank. Furthermore, it might be expected that the suction process of opening shells would require some time. In one instance, at least, in the laboratory tank a Beaufort specimen of *B. carica* opened and ate a medium sized Venus within 12 minutes.

The Busycons at Beaufort follow the patterns of food getting described previously by Colton. Suitable materials are attacked directly without any preliminary treatment; foods of this first class would

include Tagelus, dead fish, annelids, and other soft living or dead animals. Oysters, Doscinia, Macrocallista, smaller Venus, and perhaps other Pelecypods are attacked and the valves of their shells are pried apart by the insertion of the outer lip of the Busycon shell. In this case the shells of the prey are sometimes broken (Fig. 54). The third method of eating, that of shell chipping and prying, is used by both *B. carica* and *B. contrarium.* Venus and other hard shell clams are overcome by this method. Pelecypod shells both living and dead with chipped edges are often found. Busycon shells with broken or worn lips are common. The edges of Venus shells broken by action of Busycon shells are seen in Figure 55.

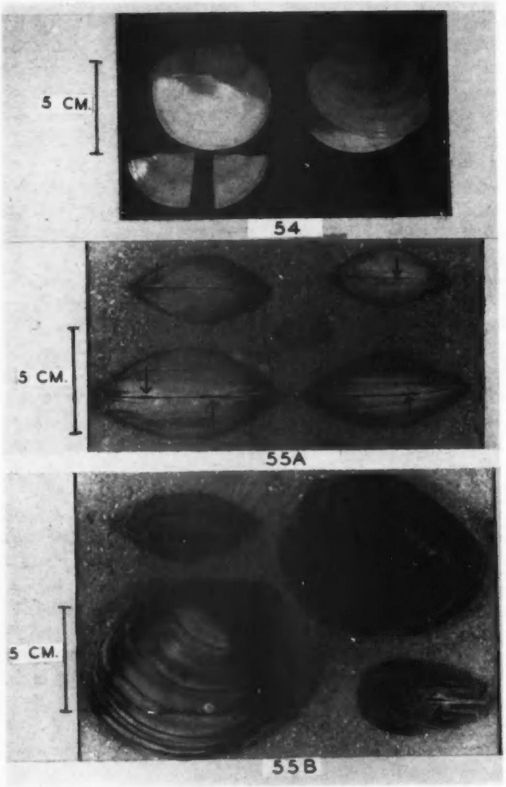


FIG. 54. Two individuals of *Dosinia discus* eaten by Busycons. The valve of one shell was broken, but the other shell was undamaged.

FIG. 55A. Venus shells from which the contents were removed by hungry Busycons. Arrows indicate regions of valves that were broken by Busycons.

FIG. 55B. Venus shells of living specimens that Busycons were unable to eat. Arrow shows chipped area broken by Busycons.

Shells of Pelecypods that have recently been eaten by Busycons, or those that are in the process of being eaten, are always covered with a thick, sticky material, probably saliva. A proteolytic enzyme has been demonstrated in Busycon saliva (Mendel and Bradley 1905). In fact this is the only protease found throughout the digestive tract of this genus. It is quite possible that this protease might aid in the process of ingestion by initiating digestion externally. The process of external digestion is known to occur in some cephalopods and a few gastropods (Yonge 1928).

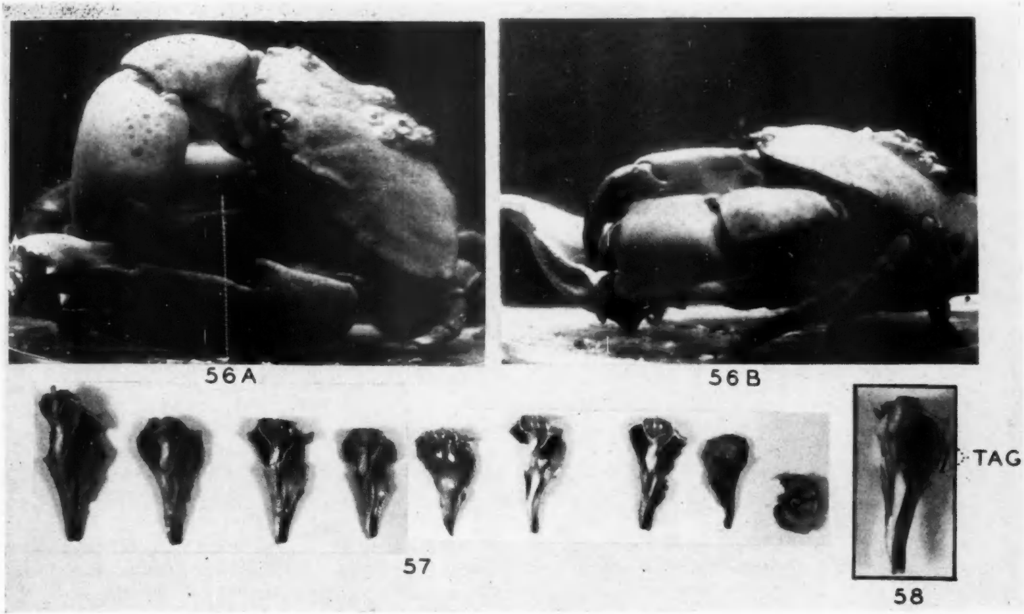
ENEMIES

Crabs and gulls are the commonest types of predators that were observed attacking and destroying Busycons. The stone crab, *Menippe mercenaria* (Say), is the most spectacular of the crabs known to eat snails for food. The activities of this crab were observed in the laboratory and the field. A medium sized stone crab collected late in July was placed in a large cylinder of sea water with several small and medium sized *Busycon caricas.* When sand was present the snails soon buried themselves. If there were no sand available the snails were unable to escape the crab. The stone crab grasped its victim with one large cheliped and rotated the shell into position so that the other cheliped could be used for crushing off portions of the shell. The outer edge of the siphon canal and mouth of the shell were chipped away and then the body whorl was cracked and finally broken. A stone crab in action is shown in Figure 56. Of seven Busycons that were placed in with a stone crab one was eaten; three were badly broken and three were not touched.

In November 1942 during an exceptionally low tide a stone crab was found within an old automobile shoe on Bulkhead Shoal. The carapace of this crab was 87.5 cms. wide. The sand surrounded by this old tire was littered with fragments of Busycon shells. There seemed to have been at least ten snails eaten. One of the larger pieces of shell had attached to it an aluminum tag which had been placed on an animal released in July about 67 meters from the home of the stone crab. It is expected that the stone crabs would be active enemies of Busycons throughout the entire year.

The hermit crabs may also be important enemies of Busycons. In the field a group of four hermits have been observed attacking a small living Busycon. Five of the recovered marked specimens were found with hermit crabs in the shells. It is not known definitely if the hermit crabs are able to kill and remove a living specimen. It may well be that the hermits removed sick, or dead, snails and then make use of the empty shells. Both *Clibanarius vittatus* (Bosc) and *Pagurus pollicaris* (Say) are commonly found inhabiting Busycon shells (Fig. 57).

Pagurus shows a preference for empty shells of *B. canaliculatum.* Clibinarius on the other hand seems to choose a new shell according to the size. One Clibinarius was observed to move from a worn *B. contrarium* to an oyster spat covered specimen of the same species, but when a clean *B. carica* was made available the hermit quickly moved in. A second hermit that was found in a small somewhat worn *B. carica* shell moved immediately into a slightly larger *B. contrarium* shell, but it later moved into a *B. carica* shell when a slightly larger one was presented to it.



FIGS. 56 A and B. Stone crab, *Menippe mercenaria* (Say), breaking up the shell of a small specimen of *Busycon carica*.

FIG. 57. Fragments of Busycon shells from the sand near the home of a stone crab.

FIG. 58. A broken shell of a specimen released on Bird Shoal. The aluminum marking tag can be seen on the right. The black border that frames the shell shows the size of the specimen at the time of release.

This same hermit moved again when it found a *B. carica* shell of even larger size.

It is quite possible that the common blue crab, *Callinectes sapidus* Rathbun, is another important enemy of Busycons, but it was never observed eating snails in the laboratory tanks, or in the field.

During the winter months of December and January particularly the herring and ring-billed gulls, *Larus argentatus smithsonianus* Coues and *Larus delawarensis* Ord, are present in the Beaufort region in large numbers. These gulls depend partly on mollusks for their food. Arca, Noetia and Busycons are commonly eaten. The gulls collect the mollusks during low tide when they are exposed on the sand and mud flats. A gull drops its prey on a road, sidewalk, or some convenient hard surface from a considerable height. The mollusk shell is broken open and the soft inner parts can then be eaten by the gulls. Often a shell has to be dropped several times before it is sufficiently broken. Occasionally the mollusks are dropped on sand where they are not broken and eaten, but die of exposure.

During December and January broken shells were observed on the road and sidewalks on Piver's Island, but they were not collected, or counted. In Table 18 the numbers of Busycons collected from the sidewalks and road near the laboratory are shown.

One marked specimen was recovered in June in the grass near the laboratory. This specimen was released the previous July at Station II. At the time of recovery the shell of this animal showed the same type of damage as that present in the shells dropped by gulls during the winter and early spring.

TABLE 18. Busycon shells dropped by gulls during the winter of 1942-1943 on the sidewalks and roadway near the Duke Marine Laboratory.

Month	*B. canaliculatum*	*B. carica*	*B. contrarium*
March	6	0	0
February	2	0	0
April	12	2	5

It was expected that some of the bottom dwelling fishes might prey on Busycons, but no confirmation of this could be obtained. The stomachs of several toadfish, flounders, sting rays, and butterfly rays were examined, but no traces of Busycon, either shells or opercula, were found.

In the Beaufort region one of the significant enemies of Busycons is man. Conchs are collected for conversion into steaks and chowder.

ECONOMICS

An ecological study of animal would be incomplete without some mention of its economic significance. The value of Busycons is slight indeed when compared with the commercially exploited pelecypods such as oysters, clams, scallops, or even mussels. If compared to other gastropods these snails are less destructive than the common oyster drills, Urosalpinx

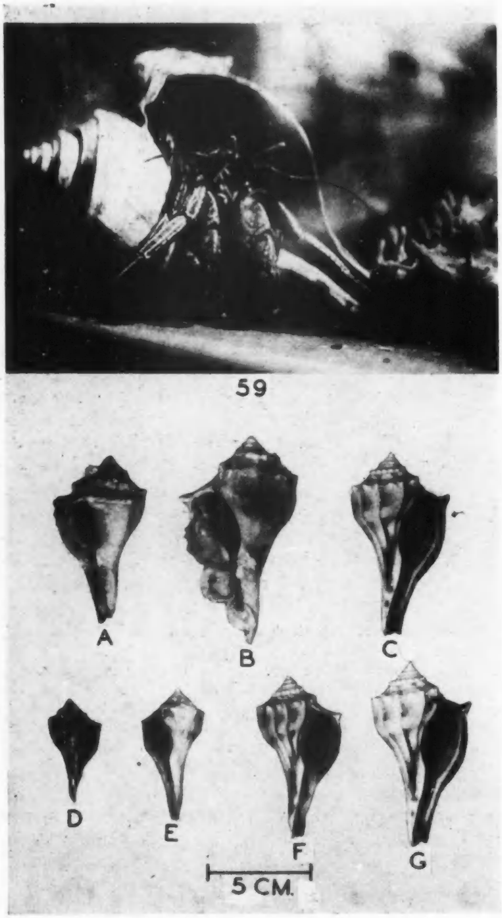


FIG. 59. A *Busycon canaliculatum* shell inhabited by *Clibanarius vittatus* (Bosc). A specimen of Clibanarius moved from shell A to B to C. A second specimen moved from D to E to F to G.

and Eupleura, since they eat mature pelecypods and do not destroy large quantities of spat. Busycons are one of the few marine snails that are used for food in this country at the present time. About a hundred years ago Busycons were sold in the New York markets for food at one dollar a hundred (DeKay 1843). At Beaufort in the summer of 1943 chopped, or ground, "conch" meat prepared from the muscular foot of Busycons could be obtained in local markets. In the spring of 1943 a single collector from Beaufort obtained 34 large specimens of *B. carica* and 5 *B. canaliculatum*. All of these animals were to be used for food. Although the collection was made on Town Marsh and Bird Shoal none of the specimens were marked. The majority of these animals were adult females that had been exposed by the unusually low tides as they were laying egg strings on the sand flats. Along the Connecticut shore *B. canaliculatum* is used as the basis for a winkle chowder (Hausman 1942). In Florida poor people are often referred to colloquially as "conchs" since they are supposed to consume gastropods such as Busycons and Strombi as articles of their diet.

In that portion of the Atlantic coast where the ranges of the common lobster and Busycons coincide these large snails are considered a nuisance because they destroy the bait placed in lobster pots.

Preserved Busycons and their egg strings are commonly stocked by biological supply houses for use in schools and universities.

Busycon shells are collected by conchologists because of their unusual size and different types of rotation. The shells are also used in a variety of ways as ornaments, lamps, flower holders, or even to outline flower beds, or decorate graves.

DISCUSSION

To be successful biologically an animal must satisfy three basic needs of food, protection, and reproduction of its kind. An ecological investigation of the common species of Busycon present in the Beaufort region reveals that in the habitats studied *Busycon carica* is the most successful, while *B. canaliculatum* and *B. contrarium* are apparently somewhat less well adapted to the conditions that prevail.

Food. The food problem of developing Busycons is solved by the presence of a large amount of yolk in the egg. As indicated by Conklin (1907) the eggs of *Busycon carica*, which average 1.7 mm. in diameter, are larger than those of *B. canaliculatum*, which average 1.0 mm. in diameter, and considerably bigger than those of various species of Crepidula, which range in size from 0.4 to 0.1 mm. in diameter. In addition to the yolk contained within the developing egg itself each capsule contains food eggs and perhaps an albumin-like material as well.

No information was obtained on the natural food of Busycons immediately after hatching. Adult animals appear to be exclusively carnivorous. They do not depend on a single type of food animal, but eat a rather varied diet that includes several species of pelecypods, annelids, and occasionally fishes and other gastropods. The foot of Busycon is broad and flat; its structure permits the animal to move with apparent effortlessness over shifting sand and soft mud in search for food. The pallial siphon directs a sample of environmental water over the osphradium. Copeland (1918) has shown that this structure is concerned with the reception of chemical stimuli so that it might be considered a primitive sort of olfactory receptor. Although the movements of Busycons are slow and inexact, they are able to locate food in the field and in the laboratory tank. The long extensible proboscis that is characteristic of these snails is adapted to the types of food eaten and the manner of feeding. This proboscis may be extended and thrust through the partially separated valves of a pelecypod shell so that food is obtained from seemingly inaccessible locations. The radula and its supporting odontophoral cartilage and attached muscles form a highly specialized and

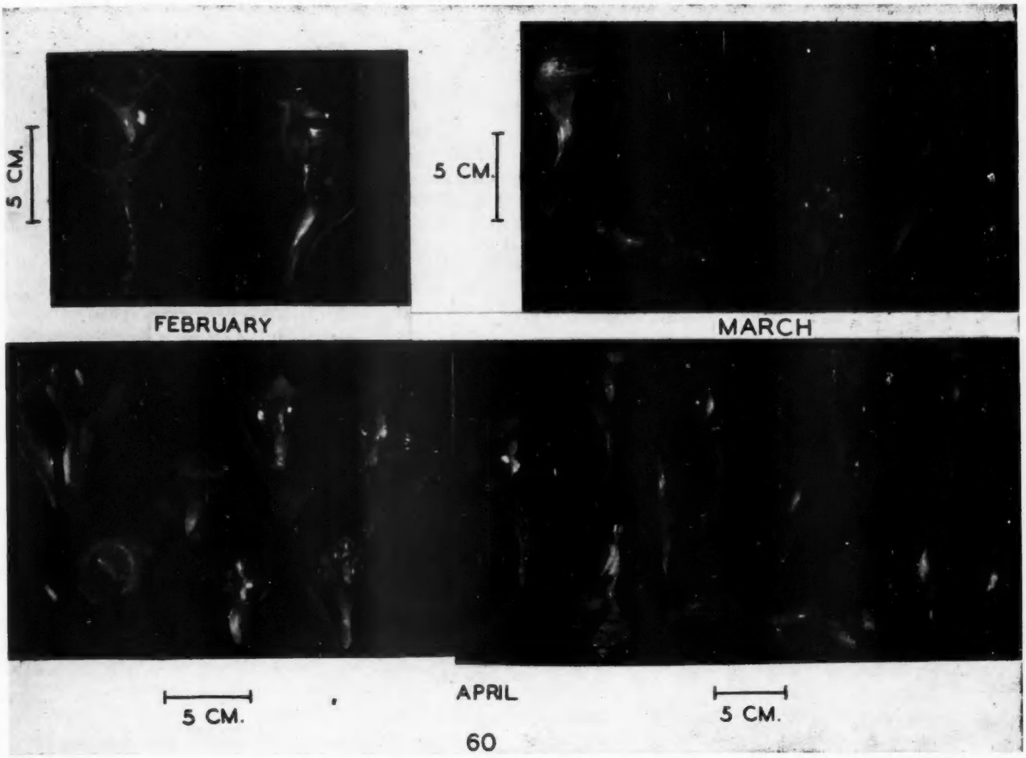


FIG. 60. Busycon shells dropped by gulls on the laboratory sidewalks during the winter of 1942-1943.

complex device for shredding, ingesting, and preparing food for subsequent chemical digestion. The action of the radula of *Busycon canaliculatum* has been described in detail by Herrick (1905). The enzymes of this snail are of the types that would be expected in an animal with a high percentage of protein foods (Mendel and Bradley 1905). The entire behavior pattern related to the feeding process makes it possible for Busycons to prey on heavy shelled pelecypods such as Venus. It can be seen that as a group Busycons are adapted not only anatomically, but also physiologically to obtain food in an environment where it is plentiful, but the competion is keen and many speedier and more sensitive animals are present.

Protection. The large size and heavy shells of adult Busycons protect them from destruction by enemies and such physical forces as pounding surf, or dehydration. The elongated siphon canal provides protection for the pallial siphon which permits the animal to remain below the surface of the sand and yet continue its function of providing the gill with a supply of oxygen containing water and bringing stimuli to the osphradium. An interesting and perhaps protective response of physiological nature is observed in the pigmentation of the foot and mantle edges in Busycons at Beaufort. It has been observed that *B. canaliculatum* is generally active at times of low light intensities during the day in winter, spring, and fall, but during the night in midsummer. On the other hand *B. contrarium* is active during the day in warmer regions when light intensities are high. *B. carica* is active both day and night depending somewhat on the season and temperatures as well as the age of the individual specimens. The foot and mantle of *B. canaliculatum* are generally quite pale grayish white; in *B. carica* there is considerable variation in pigmentation of these regions from gray to almost black; in *B. contrarium* the foot and mantle are almost always deep black. Observations by Schiedt (1904) indicate that if a valve is removed from an oyster that is exposed to light a pigment is deposited in the exposed regions. Furthermore this pigment disappears in the absence of light.

Busycons are undoubtedly most vulnerable immediately after hatching. At this stage neither the minute shells, nor the tiny opercula would be effective against enemies which would be able to ingest them whole. During development Busycons are protected from some predators by the tough capsules which surround them. Occasionally, however, entire egg strings are detached from the bottom by storms, or curious crabs, and then cast up on a beach.

The varied behavior patterns of these animals also provide them with some protection not only from enemies, but also from unfavorable environmental con-

ditions. Tidal, diurnal, and seasonal variations in activity tend to protect Busycons from excessive exposure to heat, light, or dehydration. Differences in rhythmic activity shown by the species of Busycon at Beaufort tend to segregate the species from each other. Seasonal rhythms have been observed in other genera of marine snails. Particularly the occurrence of hibernation during the winter months (Abe 1935, Hauseman, S. A. 1932, and Batchelder 1915). Hausman, S. A. (1932) has observed a daily rhythm in the salt marsh snail, *Melampus bidentatus*, which appears to be a nocturnal feeder, but occasionally moves about on foggy, or cloudy days. Tidal rhythm is shown by various species of Littorina (Haseman 1911).

The ability of Busycons to migrate is of course related to their rhythmic activity. Movement into the sand is one means by which they can escape some of their enemies. Specimens active on sunny days will retract into their shell if a shadow is cast over them. Migration has been observed by other workers in several marine snails, but not for Busycons (Batchelder 1915), Gowanloch 1926, Gowanloch and Hayes 1926, Suzuki 1934, and Willcox 1905). *Busycon carica* at Beaufort was observed to move from 0 to 40 meters in a day. A rate of 1.2 to 12 yards a day was reported for Nassarius and Littorina (Batchelder 1915) Gowanloch (1926) reports that *Buccinum undatum* migrated an average of 8.3 meters in five weeks. A rate of 2 meters a day was reported for *Nerita japonica* (Suzuki 1934). A comparison of these figures would indicate that compared with other snails Busycons are rather active animals.

The material obtained on the relationship between Busycons and their environmental temperature indicate that *B. canaliculatum* is less sensitive to low temperatures than *B. carica*. On the other hand *B. carica* is less sensitive to higher temperatures than *B. canaliculatum*. The lower limit of temperature toleration for *B. carica* was about 10° C.; that for *B. canaliculatum* about 8.5°. The upper limit for *B. carica* was about 35° C. while that for *B. canaliculatum* was 31.5° Limits were not determined for *B. contrarium* because of the small number collected it was felt that they would not be significant. The oyster drill, *Urosalpinx cinera* Say, a common Beaufort species, is inactive below 10° C.; does not feed until 15° C.; spawns at temperatures above 20° (Federighi 1931).

Related to the problem of temperature tolerations is the question of range of distribution. According to Johnson (1934) *B. canaliculatum* is found south of Cape Cod to St. Augustine, Florida; *B. carica* also ranges from the southern shore of Cape Cod to a point somewhat south of St. Augustine, Cape Canaveral, Florida. *Busycon contrarium* is reported by Johnson (1934) to occur from North Carolina south to Florida and Texas. The report of Wood and Wood (1927) seems to show that *B. contrarium* is occasionally, at least, present north of North Carolina in the southern part of New Jersey. Other reports of the distribution of these species seem to show that the ranges cited by Johnson are too short. The range of *B. canaliculatum* is given as Beverly, Mass., to the Gulf of Mexico and that for *B. carica* as Cape Cod to St. Thomas, West Indies (Sumner, Osburn, and Cole 1911). In the Woods Hole region even though both *B. canaliculatum* and *B. carica* are present their distribution is not identical. *B. carica* occurs in greater numbers in regions of high temperature and low densities (Sumner, Osburn, and Cole 1911). Similarly at Beaufort the density of population of the three species of Busycon studied was not uniform through the habitats investigated. *Busycon carica* was found in large numbers in the shallow water south of Town Marsh toward Bird Shoal. The same region supported a moderate sized population of *B. canaliculatum*. This second species, however, was not as active during the warmer months as *B. carica*. *B. contrarium* seemed to be present in deeper water and only at higher temperatures.

Reproduction. The slight sexual dimorphism that is present in *Busycon carica* may represent an adaptation for differences in sexual function. For the females, which produce eggs and egg strings, a large size is advantageous for it permits formation and storage of these essential materials. In the males on the other hand a smaller size might well be an adaptation to permit greater freedom of movement and aid in seeking out females. Morse (1876) described a diminutive form of *Buccinum undatum* male in which both the shell structure and size varied from that of the female. He felt that this was a definite case of natural selection.

The periodicity of ovoposition in mollusks has been studied by Pelseneer (1927). He concludes that as a general rule most mollusks spawn at night Busycons, however, do not seem to show any diurnal rhythm in the production of egg strings. Once a string has been started it is formed at a fairly constant rate of about 12 to 14 cases per day; the time of day seems to have little influence on the rate of production. The rate of production of strings may be influenced by the temperature. In the Beaufort region not more than 5, or 6, days would be required for the production of a single string, but a report has been found (anon. 1910) that in the Massachusetts region 8 days are necessary for the production of a single string. Although there appears to be no diurnal rhythm in spawning there is a definite seasonal rhythm. At Beaufort there are two breeding and spawning periods each year; one in the spring and a second in the fall. The critical temperature for egg string production seems to be about 20° C.

The numbers of eggs produced by different animals depend on the amount of protection that is afforded the eggs and young following fertilization. A single female *Busycon carica* can produce from 4,000 to 6,000 eggs in a single string. This is somewhat less than the numbers produced by *Purpura lapillus*, which lays 300-1,000 in each capsule and forms from 6 to 31 capsules at one time (Moore 1938). Another small marine snail that deposits its eggs in capsules, *Urosalpinx cinera*, has been reported to produce about 28 capsules per season with an average of 9

eggs per capsule, but only 58% of the eggs hatch into larvae so that the numbers of larvae produced is quite small (Federighi 1931). Another marine snail produces about 1,000 eggs per capsule and one hundred, or more, capsules per clump, but this species, *Thais haemastoma*, hatches as a free swimming veliger (Burkenroad 1931). A very large marine snail, *Fasciolaria gigantea*, produces as many as 30,000 young in a single clump of capsules (Johnson 1929). It has been shown that *Fasciolaris tulipa*, may produce as many as 600-800 eggs per capsule, but of these only a few develop; the remainder are eaten by the normal larvae (Burger and Thornton 1935). Among various species of Crepidula the number of eggs produced by a single female vary in number from 180 to 13,200 (Conklin 1897, Orton 1912). In this species the developing eggs are afforded some protection by the shell of the female under which they develop. The sea hare, *Tethys californicus*, produces over 478 million eggs in a six months' period (Mac Ginitie 1934). Compared with other gastropods Busycons seem to produce only a moderately large number of eggs. This number is undoubtedly kept small because of the protection provided by the capsule for the developing individuals.

Growth. The examination of marked and measured specimens of *Busycon carica* indicated clearly that the process of growth in these animals is markedly irregular. Even immature specimens showed no change in size after a year, or two, in the field under apparently favorable conditions. Coe (1942) reports that Crepidula, a non-predatory gastropod, may live for a year or more without any considerable increase in dimensions.

The validity of the practice of using so-called growth rings of mollusk shells as a means for estimating the age of specimens has been questioned by several investigators (Coe 1942, Orton 1926, 1928, Rao 1936, and Stephen 1928). Various factors may interrupt growth and produce disturbance rings in the shells of both gastropods and pelecypods. Lines of this type cannot be distinguished from the rings of growth produced by normal interruption of growth that occurs during the winter (Orton 1926). The number of growth, or disturbance rings, produced during a single year varied in Busycons from none to two. The number of shoulder spines is no indication of the rate of growth, since the formation of a single spine may require from 3 to 17 months. The growth ring method of age determination has been applied successfully in the limpet, *Acmaea dorsusoa* Gould (Abe 1932). If the rate of growth of Busycons could be measured under natural conditions for the first year it might be possible to estimate the ages of specimens of different sizes.

It seems probable that there is a difference in rate of growth in male and female Busycons. The rate of growth is somewhat slower in smaller specimens than in either medium, or large ones. Additional data are needed before a sexual difference in growth rate can be demonstrated clearly. The rate of growth is commonly faster for female gastropods than it is for males of the same species (Coe 1942, Cole 1942, Moore 1936, Rao 1936).

There is no doubt that in *Busycon carica* growth is periodic in character and not a constant process. The number of specimens in which growth did occur was so small and the periods of time involved were of such a length that it was impossible to determine the factors necessary for initiation of growth. It is known that in some gastropods such as Patella and Crepidula, there is a seasonal difference in growth rate (Orton 1928, Coe 1942), but in Trochus no such change was found in the growth rate (Rao 1936). There is a possibility that the period of greatest growth follows the breeding season. It may also be related to the quantity and quality of food that is available. Engle (1942) and Moore (1936) have shown that the rate of growth and type of shell produced by marine gastropods depends on the sort of food that is eaten.

An additional factor that may have influenced the results obtained in the observations on growth of *Busycon carica* was the method used in these studies. Collections were made over a rather large area on Town Marsh and Bird Shoal flats. For convenience these specimens were mixed and carried to the laboratory for marking and measurement and then returned to a few stations. Such a procedure would tend to concentrate the snails in regions near the points of release. This facilitates recovery of marked specimens, but may inhibit growth through crowding, lack of preferred foods, increased spread of parasites in contaminated laboratory tanks. On the other hand the large numbers of Tagelus available in the laboratory tanks may have made it possible for the snails to obtain food and grow at a time when they would not have eaten under normal field conditions. The factor of population density is an important one in the regulation of growth in mollusks (Forbes and Crampton 1942, Stephen 1928). The importance of parasitic infections in relation to growth of mollusks has been demonstrated clearly by the work of Rothschild (1936, 1941). She has shown that accelerated growth and even gigantism can be produced by infections of trematode parasites that may produce changes through destruction of gonads and other glands in both *Littorina neritoides* and *Peringia ulvae*.

The relationship between Busycons and other animals in their environment may be summarized by means of a food chain. The one shown in Figure 61 has been constructed from the results of the present study. The most important single food of adult Busycons appears to be pelecypods of various species. In the Beaufort region they do not seem to constitute a serious menace as far as either osyters, or clams, of economic importance are concerned because there are plentiful supplies of several non-economic species of pelecypods available. Busycons prefer Tagelus, Doscinia, and even Chione as they are easier to feed upon than either oysters or Venus. At Beaufort one of the most significant enemies of adult Busycons is man. The collection of large numbers of adult fe-

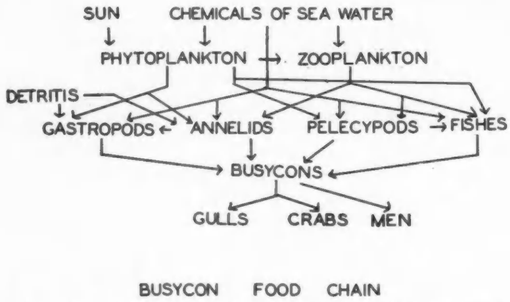


FIG. 61. A food chain based on observations of Busycons at Beaufort, N. C.

males during the breeding season for human food might seriously deplete the population if such a practice was carried out for several years.

As predators Busycons are not members of any definite association of animals in the littoral region. They are able to wander from one type of habitat to another depending on the conditions of food supply, enemies, or temperature, and salinity that obtain. They are often present in muddy sand near oyster beds, but they are more plentiful in areas of sandy mud where Venus, Dosinia, or Tagelus are found. Even where they are most plentiful they do not seem to play a controlling role in the life of the community. Occasionally, however, a large Busycon shell provides a place of attachment for many sessile organisms in much the same way that a pile permits the establishment of an association of animals. In this sense the Busycon would indeed be the dominant member of the community since its habits and habitat would determine the characteristics of the entire association. An interesting problem that suggests itself in this connection would be the determination of the causes for differences in animals and plants that are found on Busycon shells that are inhabited by crabs as compared with those shells that contain their original owners. The shells occupied by crabs are often covered by oyster spat and Crepidula shells neither of which are commonly found on living snail shells. It is quite possible that the major differences are dependent on the fact that the snails remain buried for rather long periods under the sand of the bottom while the crabs are more active and do not remain buried for such long periods of time.

The populations of the three common species of Busycon show very distinct characteristics in the habitats in which they were studied at Beaufort, North Carolina. The *B. carica* population is quite juvenile in character; such large numbers of young would indicate that it is actively replacing itself and that the region studied represents a region of reproductive distribution for that species. The *B. contrarium* population on the other hand is somewhat senile in character with a preponderance of older individuals and only an occasional young specimen. This population seems to represent what may be a sterile distribution at least in the habitats investigated most closely. The remarkable feature of the *B. canaliculatum* population is the uniformity of the sample obtained. This species shows a predominance of individuals of moderate size in the areas in which collections were made. A comparison of the numbers and sizes of specimens of three species of Busycons common in the Beaufort region with those reported from other regions indicates that even though these three species show overlapping ranges they have slight, but marked differences in tolerations, habits, and rhythms. *Busycon canaliculatum* is characteristically a more northern species; it attains larger size and a greater density of population along the coast of southern New England. *B. carica*, on the other hand, in so far as information is available reaches its greatest development in both numbers and size in the Beaufort region. For this reason it might be considered as typically a middle Atlantic species. Finally, *B. contrarium* acquires its maximum growth and greatest concentration in numbers along the Florida coast; it is a normal Southern Atlantic species.

The analysis of the species of Busycon at Beaufort according to the proportions of their shells, that is, the ratio of length to width suggests several possibilities. The results obtained for *Busycon canaliculatum* may be interpreted as indicating that there are two distinct types of specimens in the population sample examined. This might be represented by mature females in one group and younger females, mature males, and perhaps juvenile specimens in the other group. On the other hand the larger group might represent normal individuals with the smaller group consisting of diseased animals infected by some trematode parasite. In the case of *B. carica* the comparison of the percentages of specimens with shells showing different length/width ratios indicates that there are perhaps three distinct groups of individuals in the Beaufort population either mature females, mature males with younger females, and finally juvenile of both sexes. With *B. carica* there is also the possibility that the Beaufort population represents a mixture of *B. carica* and *B. eliceans*. This is a problem that can only be settled by the study of large samples of shells from different habitats along the Atlantic Coast. Similarly with *B. contrarium* there seems to be a marked heterogeneity in the population sample studied. Again the results obtained seem to warrant further work in regard to the taxonomy of the entire genus. With both *B. canaliculatum* and *B. contrarium* the number of individuals of the sample measured were rather small.

SUMMARY

1. A comparison of measurements of shells of living specimens of *Busycon carica* (1,000), *Busycon canaliculatum* (70), and *Busycon contrarium* (50) indicates that the populations of these marine snails in Beaufort, North Carolina, are distinct in character. The *B. carica* population is juvenile in nature with a predominance of immature individuals. The population of *B. contrarium* is quite variable and some-

what senile with more mature and fewer younger specimens. The *B. canaliculatum* population is remarkably uniform with a preponderance of moderate sized individuals.

2. The following mean values were found to be characteristic of the Busycons of the Beaufort region: for *B. canaliculatum* a length of 12.4 cms., width of 6.4 cms., shell proportion (w/1) 1.95, and volume 113 mls.; for *B. carica* length of 9.0 cms., width 5.0 cms., width-spines 4.5 cms., shell proportion (1/w-s) 2.06, and volume 73.6 mls.; for *B. contrarium* a length of 14.4 cms., a width of 7.9 cms., a width-spines of 6.6 cms., shell proportion (1/w-s) of 2.07, and a volume of 176 mls.

3. In the habitats studied at Beaufort, North Carolina, from June 1942 to June 1943 the relative abundance of the three species of Busycons present can be expressed by the ration of 1 *(B. contrarium)* : 2 *(B. canaliculatum)* : 33 *(B. carica)*.

4. A group of 973 specimens of *B. carica* were marked, measured, and released at different stations in the Beaufort Harbor during 1942 and 1943. By the summer of 1946 a total of 10.3% of these specimens had been recovered. Of those released 8.9% were living and 1.4% were dead at the time of recovery.

5. The density of the population of *B. carica* on the Town Marsh-Bird Shoal flats in the summer of 1943 was estimated at one individual for each area 8.9 feet square.

6. Seasonal and diurnal rhythms of activity of Busycons were observed. *B. contrarium* is characteristically active during the warmer months and during the day. *B. canaliculatum* is most active at cooler temperatures, that is, at night during warmer months, either night, or day, during the spring and fall, and during the day in the winter months. *B. carica* is active both day and night except during extremely cold, or excessively hot, weather. All species of Busycon are more active for a short time before low tide and after the tide has begun to rise than at other times of day, or night.

7. The sex ratio of males to females in *Busycon carica* varied from 1:1 to 2:1, but for *B. canaliculatum* the variation was more pronounced from 1:4 to 4:1. In the Beaufort region copulation was found to occur with *Busycon carica* in March, August, and September, with *B. canaliculatum* during the same months, but usually later in the month than in the case with *B. carica*. Copulation of individuals of *B. contrarium* was observed only in August. Freshly laid egg strings are commonly found during May, June, September, October, and November. The egg strings vary in length from less than 20 to over 150 cases per string. The usual number of eggs in a single capsule is between 30 and 50. An entire string may contain from 4,000 to 6,000 eggs.

8. Algae, bryozoa, tube-dwelling annelids, sedentary gastropods, and barnacles were found to be common consortes of the outer surface of shells of living Busycons.

9. The size ranges of common pelecypods eaten by Busycons were determined. Tagelus, Chione, Venus, Dosinia, and Modiolus are some of the common food animals of Busycons. The total number of teeth in the radulae of Busycons was found to vary from 270-400 for *B. carica*, 350-425 for *B. contrarium*, and 450 for *B. canaliculatum*. The number of teeth present is consistent with the carnivorous diet of the members of the genus.

10. Man, crabs, and gulls constitute the chief enemies of Busycons.

11. Growth was observed in 52% of the recovered living specimens of released *Busycon carica*. The formation of a single shoulder spine requires from 94 to 501 days. The growth, or disturbance, lines formed during a single year may vary from none to three. The maximum rate of shell growth takes place in the center of the lip, or in the shoulder region of the shell. For small specimens the mean percentage increase in length per hundred days is 1.46%; with specimens of medium size it is 2.8%; for large specimens 2.12% and for very large specimens 2.7%.

BIBLIOGRAPHY

Abe, N. 1935. The age and growth of the limpet, Acmaea dorsusoa Gould. Sci. Rept. Tôhoku Imp. Univ. **7:** 347-363.

Allee, W. C. 1923. Studies in marine ecology. I. The distribution of common littoral invertebrates of the Woods Hole region. Biol. Bull. **44:** 167-191.

Anonoymous. 1910. Fulgur canaliculatum spawning. Nautilus **24:** 12.

Batchelder, C. H. 1915. Migration of Ilynassa obsoleta, Litorina litorea, and Litorina rudis. Nautilus **29:** 43-46.

Bergmann, W. 1934. Contributions to the study of marine products. II. The sterols of mollusks. Jour. Biol. Chem. **104:** 317-328.

Bumpus, H. C. 1898. The breeding of animals at Woods Hole during the month of May, 1898. Sci. N. S. **8:** 58-60.

Burger, J. W., & C. S. Thornton. 1935. A correlation between the food eggs of Fasciolaria tulipa and the apyrene spermatozoa of prosobranch mollusks. Biol. Bull. **68:** 253-357.

Burkenroad, M. D. 1937. Notes on the Louisiana conch, Thais haemastoma Linn., in its relation to the oyster, Ostrea virginica. Ecol. **12:** 656-664.

Clench, W. J. 1939. Mollusks that "muscle in." New Eng. Nat. **3:** 12-13.

Coe, W. R. 1942. Influence of natural and experimental conditions in determining shape of shell and rate of growth in gastropods of the genus Crepidula. Jour. Morph. **71:** 35-47.

Cole, H. A. 1941. Sex-ratio in Urosalpinx cinerea, the American oyster drill. Nature **147:** 116.
1942. The American whelk tingle, Urosalpinx cinerea (Say), on British oyster beds. Jour. Mar. Biol. Assoc. **25:** 477-508.

Colton, H. S. 1905. Sexual dimorphism in Strombus pugilis Linne. Nautilus **18:** 138-140.
1908. How Fulgur and Sycotypus eat oysters, mussels, and clams. Proc. Acad. Nat. Sci. **60:** 3-10.

Conklin, E. G. 1897. The embryology of Crepidula. Jour. Morph. **13:** 1-226.
1898. Environmental and sexual dimorphism in Crepidula. Proc. Acad. Nat. Sci. Phila. **40:** 435-444.
1907. The embryology of Fulgur: A study of the influence of yolk on development. Proc. Acad. Nat. Sci. Phila. **59:** 320-359.

Cooke, A. H. 1895. Mollusca. Cambridge Natural History **3:** 1-459.

Copeland, M. 1918. The olfactory reactions of the marine snails Alectrion obsoleta (Say) and Busycon canaliculatum (Linn.). Jour. Exp. Zool. **25:** 177-227.

Coues, E. 1871. Notes on the natural history of Fort Macon, N. C., and vicinity (No. 1). Proc. Acad. Nat. Sci. Phila. **23:** 120-131.

Dakin, W. J. 1912. Buccinum. Liverpool Mar. Biol. Com. Mem. **20:** 1-123.

Dall, W. H. 1889. A preliminary catalogue of the shell-bearing marine mollusks and brachiopods of the southeastern coast of the United States, with illustrations of many of the species. Bull. U. S. Nat. Mus. No. **37:** 1-221.

DeKay, J. E. 1843. Zoology of New York. Part V. Mollusca. Albany, 1-271.

Drew, G. A. 1936. (J. A. Dawson and L. P. Sayles.) A laboratory manual of invertebrate zoology. Rev. ed. Phila., 1-276.

Engle, J. B. 1942. Growth of the oyster drill, Urosalpinx cinerea, Say, feeding on four different food animals. Anat. Rec. **84:** 505.

Federighi, H. 1931. Studies on the oyster drill (Urosalpinx cinerea, Say). Bull. U. S. Bur. Fish. **47:** 85-115.

Forbes, G. S., & H. E. Crampton. 1942. The effect of population density upon growth and size in Lymnaea palustris. Biol. Bull. **83:** 283-289.

Gould, A. A. 1841. Report on the Invertebrata of Massachusetts, comprising the Mollusca, Crustacea, Annelida, and Radiata. Cambridge xiii + 373.

Gowanloch, J. N. 1926. Contributions to the study of marine gastropods. II. The intertidal life of Buccinum undatum, a study in non-adaptation. Contr. Canad. Biol. & Fish. **3:** 169-177.

Gowanloch, J. N., & F. R. Hayes. 1926. Contributions to the study of marine gastropods. I. The physical factors, behavior, and intertidal life of Littorina. Contr. Canad. Biol. & Fish. **3:** 135-166.

Gutsell, J. S. 1930. Natural history of the bay scallop. Bull. U. S. Bureau Fish. **46:** 569-632.

Hackney, A. G. 1944. Note on Busycon carica (Gmelin). Nautilus **57:** 143.
1944. List of Mollusca from around Beaufort, N. C., with notes on Tethys. Nautilus **58:** 56-64.

Haseman, J. D. 1911. The rhythmical movements of Littorina littorea synchronous with ocean tides. Biol. Bull. **21:** 113-121.

Hausman, L. A. 1942. Use of Busycons as food. (Personal communication.)

Hausman, S. A. 1932. A contribution to the ecology of the salt marsh snail, Melampus bidentatus Say. Amer. Nat. **69:** 541-545.

Herrick, J. C. 1906. Mechanism of the odontophoral apparatus in Sycotypus canaliculatus. Amer. Nat. **40:** 707-737.

Jacot, A. P. 1921. Some marine molluscan shells of Beaufort and vicinity. Jour. Elisha Mitchell Sci. Soc. **36:** 129-145.

Johnson, C. W. 1903. Some notes on the genus Fulgur. Nautilus **17:** 73-75.
1929. The egg capsules of Fasciolaria gigantea Kiener. Nautilus **43:** 63.
1934. List of the marine Mollusca of the Atlantic Coast from Labrador to Texas. Proc. Boston Soc. Nat. Hist. **40:** 1-204.

Mac Ginitie, G. E. 1934. The egg-laying activities of the sea hare, Tethys californicus (Cooper). Biol. Bull. **67:** 300-303.

McDougall, K. D. 1943. Sessile marine invertebrates of Beaufort, N. C. Ecol. Monogr. **13:** 321-374.

Mendel, L. B., & H. C. Bradley, 1905. Experimental studies on the physiology of the molluscs. Amer. Jour. Physiol. **13:** 17-29.

Moore, H. B. 1936. The biology of Purpura lapillus. I. Shell variations in relation to environment. Jour. Mar. Biol. Assoc. **21:** 61-89.
1938. The biology of Purpura lapillus. II. Growth. Jour. Mar. Biol. Assoc. **23:** 57-66.

Morse, E. S. 1876. On a diminutive form of Buccinum undatum male: case of natural selection. Proc. Boston Soc. Nat. Hist. **18:** 284-286.
1921. Observations on living gastropods of New England. Peabody Mus., Salem, Mass., 1-28.

Orton, J. H. 1912. An account of the natural history of the slipper-limpet (Crepidula fornacata). Jour. Mar. Biol. Assoc. N. S. **9:** 437-443.
1926. On the rate of growth of Cardium edule. Part 1. Experimental observations. Jour. Mar. Biol. Assoc. **14:** 239-279.
1928. Observations on Patella vulgata. Part II. Rate of growth of shell. Jour. Mar. Biol. Assoc. **15:** 863-874.

Osburn, H. L. 1887. Notes of Mollusca obtained at Beaufort, N. C. Stud. Biol. Lab. Johns Hopkins Univ. **4:** 64-81.

Pearse, A. S. 1936. Estuarine animals at Beaufort, North Carolina. Jour. Elisha Mitchell Sci. Soc. **52:** 174-222.

Pearse, A. S., H. J. Humm, & G. W. Wharton. 1942. Ecology of sand beaches at Beaufort, North Carolina. Ecol. Monogr. **12:** 135-190.

Pelseneer, P. 1927. Periodicité diurne dans la ponte chez les mollusques. Ann. Soc. Zool. Belg. **57:** 34-56.
1928. La variabilite relative des sexes d' apres des variations chez Patella, Trochus, et Nassa. Acad. Roy. Belgique Cl. Sci. Mem. Coll. in 8° **10:** 1-52.

Perkins, G. H. 1869. Molluscan fauna of New Haven. A critical review of the marine, freshwater, and land Mollusca of the region, with descriptions of many of the living animals and of two new species. Proc. Boston Soc. Nat. Hist. **13:** 109-136.

Perry, L. M. 1940. Marine shells of the southwest coast of Florida. Bull. Amer. Paleont. No. 95. 1-260.

Pratt, H. S. 1935. A manual of the common invertebrate animals exclusive of insects. Rev. ed. Phila. xviii + 854.

Rao, H. S. 1936. Observations on the rate of growth and longevity of Trochus niloticus Linn. in the Andaman Islands. Rec. Ind. Mus. Calcutta **38:** 473-498.

Redfield, A. C. 1934. The hemocyanins. Biol. Rev. **9:** 175-212.

Reese, A. M. 1942. The old star-fish clam question. Science N. S. **96:** 513-515.

Richards, H. C. 1936. Some shells from the North Carolina "Banks." Nautilus **49:** 130-134.
1938. Animals of the seashore. Boston, 1-273.

Robertson, J. D. 1941. The function and metabolism of calcium in the Invertebrata. Biol. Rev. **16:** 106-133.

Rogers, J. E. 1920. The shell book. New York, xxi + 485.

Rothschild, M. 1936. Gigantism and variation in Peringia ulvae Pennant 1777, caused by infection with larval trematodes. Jour. Mar. Biol. Assoc. **20:** 537-546.
1941. The effect of trematode parasites on the growth of *Littorina neritoides* (L.). Jour. Mar. Biol. Assoc. **25:** 69-80.

Schiedt, R. C. 1904. Some phenomena of animal pigmentation. Amer. Jour. Physiol. **10:** 365-372.

Smith, B. 1905. Senility among gastropods. Proc. Acad. Nat. Sci. Phila. **57:** 345-361.
1909. Note on the morphology of Fulgur. Proc. Acad. Nat. Sci. Phila. **61:** 369-372.
1939. Type specimen of Busycon perversum (Murex perversus Linne). Nautilus **53:** 23-26.
1943. Two abnormal Busycon shells. Palaeontographica Amer. **3:** 93-96.
1944. Two spine rows in a Florida Busycon contrarium. Palaeontographica Amer. **3:** 3-9.

Smith, S. 1862. On the Mollusca of Peconic and Gardiner's Bays, Long Island, New York. Ann. Lyc. Nat. Hist. N. Y. **7:** 147-168.

Stephen, A. C. 1928. Notes on the biology of Tellina tenuis da Costa. Journ. Mar. Biol. Assoc. **15:** 683-702.

Stimpson, W. 1860. A trip to Beaufort, N. Carolina. Amer. J. Sci. (2) **29:** 442-445.
1865. On certain genera and families of zoophagous gasteropods. Amer. Jour. Conch. **1:** 55-64.

Sumner, F. B., R. C. Osburn, & L. J. Cole. 1913. A biological survey of the waters of Woods Hole and vicinity. Bull. U. S. Bur. Fisheries **31:** 5-442; 547-794.

Suzuki, S. 1934. Notes on the behavior of Nerita japonica Dunker. Sci. Rept. Tôhoku Imp. Univ. (4) **9:** 297-314.

Thompson, M. T. 1890. The breeding of animals at Woods Hole during the month of September, 1898. Sci. **9:** 581-583.

Warren, S. 1916. Feeding habits of Busycon. Nautilus **30:** 66-68.

Wilhelmi, R. W. 1944. Serological relationships between Mollusca and other invertebrates. Biol. Bull. **87:** 96-105.

Willcox, M. A. 1905. Biology of Acmaea testudinalis Müller. Amer. Nat. **39:** 325-333.

Wood, A. E., & H. E. Wood. 1927. A comparative study of the marine mollusks of Cape May County, New Jersey. Nautilus **41:** 8-18.

Yonge, C. M. 1928. Feeding mechanisms in the invertebrates. Biol. Rev. **3:** 21-76.

ANALYSIS OF REPEAT RECORDS OF BANDED WHITE-THROATED SPARROWS

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ANALYSIS OF REPEAT RECORDS OF BANDED WHITE-THROATED SPARROWS

THE PROBLEM

Each year bird banders throughout the country band thousands of white-throated sparrows *(Zonotrichia albicollis)*, yet most of these banders, particularly those located between the summer and winter ranges of the species, never get a single return or recovery on their birds. As a result, most of this banding is done in vain as far as any contribution to our knowledge of the species is concerned. On the other hand, white-throats enter traps readily, and every bander who bands appreciable numbers of this species gets repeats on a relatively large percentage of his birds. This raises the question, can these repeat records be used to give us any information on the white-throat's migratory behavior? If they can, then there is an abundance of data in the files of bird banders from which much can be learned about this and other migratory species.

At the writer's banding station the white-throat is strictly a transient; it neither breeds nor winters in this area. In the case of such transient species it would seem that repeat records should throw light on several points: (1) how long individual birds stay at the station during their stopovers; (2) how the number of individuals present at the station varies from day to day, and how many individuals pass through the station in a season; and (3) what may be called the *stopover range*, i.e., the area over which an individual bird ranges during the stopovers in its migration. Repeat records should show any difference that may exist in the migratory behavior of different sex and age groups, early and late migrants, and in the migration in different seasons. The data from repeats should give us a clearer concept of many phases of bird migration that are at present little understood.

A survey of the literature shows that few banders of transient species like the white-throat have made any attempt to analyze their repeat records, and none has ever published an analysis with all of the foregoing points in mind. Most papers based on banding data have been concerned mainly with returns and recoveries, with little or no concern with repeats; accounts of repeats are usually mere tabulations of data with no attempt at interpretation. The present writer has seen no papers on the problem of the stopover range of a passerine bird, and only a few which have used banding data to estimate bird numbers. This analysis of repeat records represents what appears to be a new approach to the solution of certain problems of bird migration and bird behavior, and indicates what may be done with a large amount of data that up to the present time has been little used.

The writer wishes to express his appreciation to all those who have been of assistance in this study, particularly to Mr. Douglas L. Stancombe, who has helped operate the banding station during the past few seasons, and to Dr. Earl L. Green of the Department of Zoology and Entomology, Ohio State University, and to Dr. F. W. Preston, of the Preston Laboratories, Butler, Pennsylvania, for their helpful suggestions regarding the use of statistical procedures.

THE BANDING STATION

The data reported in this paper were obtained at the writer's banding station, which has been operated on the campus of Ohio State University since 1938. Because of the pressure of other duties, and an absence on military leave, there have been a few seasons during this period when little or no trapping was done. The traps have been located principally in the University Botanical Garden, an area of about eight acres located in the southwestern part of the campus. This area is covered with a fairly dense growth of trees and shrubs that provide excellent food and cover for birds. To the west of the garden is the University Athletic Field, a level flood plain area that extends to the Olentangy River, about one-half mile distant. The campus on other sides of the garden is a park-like area containing numerous buildings, large trees, small patches of shrubbery, and open lawns.

Three types of traps have been used, drop traps, funnel traps, and various automatic traps operated by a trigger mechanism. The funnel traps consisted of cloverleaf, maze, and government sparrow traps; the automatic traps consisted of various types of cage traps with a side opening, and chardonneret traps. The traps were baited with a grain mixture, and were visited several times daily.

The number of traps in operation each season varied from 3 to 19 (average, 9) in the spring seasons, and from 4 to 15 (average, 8)in the fall seasons. The funnel traps proved most successful for catching white-throats.

THE ANALYSIS

Introduction

The analysis of repeat data is essentially a problem in statistical analysis. For the most part it involves tabulating data and getting summaries, conceiving interpretations of these summaries, then applying whatever mathematical procedure may appear applicable to arrive at or to support the interpretations. Unfortunately there are many unknown factors, and many conclusions drawn must be regarded as tentative. This analysis should serve as a guide for planning

trapping methods or experimental work designed to test some of these conclusions.

Adults have been differentiated from immatures on the basis of their brighter markings; this criterion is probably not too reliable, and it is quite possible that some of the birds herein reported have not been correctly aged. The skull examination method of aging white-throats, suggested by Miller (1946), has not been used. No attempt has been made to distinguish the two sexes.

The ease of analyzing banding data depends to a considerable extent on the form in which the data are organized. The records for any given season can best be analyzed after first being summarized in the form shown in Figure 1. This gives a more or less graphic picture of the data, and various summaries are easily obtained once the data are so organized.

The writer's banding and repeat data are summarized in Table 1. There has been considerable variation in the numbers of birds handled in different seasons, and the data for some seasons are too meagre for any sort of analysis. The percentage of banded birds which repeated (49.62%) is similar to that obtained by banders who have banded larger numbers of birds; e.g., Commons (1938) had 50.23% of 1,394 birds repeat, and Middleton (1939) had 49.79% of 3,451 birds repeat.

A slightly greater proportion of the immatures than the adults repeated (52.78% as compared with 47.69%), and a slightly greater proportion of the banded birds repeated in the fall than in the spring (50.39% as compared with 48.55%), but these differences are not significant.

The proportion of the banded birds which repeat may serve as an index of the birds' length of stay,

TABLE 1. Summary of White-throated Sparrow banding at Ohio State University.

Season		Number Banded			Birds Repeating					
					Adults		Immatures		Total	
		Ad.	Imm.	Total	No.	Percent	No.	Percent	No.	Percent
Spring	1938	0	3	3	0	0.00	0	0.00	0	0.00
	1939	4	8	12	3	75.00	2	25.00	5	41.67
	1940	33	22	55	17	51.52	12	54.55	29	52.73
	1941	6	7	13	3	50.00	3	42.86	6	46.15
	1942	5	6	11	0	0.00	1	16.67	1	9.09
	1943	22	27	49	8	36.36	13	48.15	21	42.86
	1944	27	19	46	17	62.96	13	68.42	30	65.22
	1946	15	8	23	2	13.33	2	25.00	4	17.39
	1947	33	31	64	17	51.52	21	67.74	48	59.38
	Total	145	131	276	67	46.21	67	51.15	134	48.55
Fall	1938	9	17	26	4	44.44	10	58.82	14	53.85
	1939	10	2	12	8	80.00	1	50.00	9	75.00
	1940	37	10	47	15	40.54	4	40.00	19	40.43
	1941	11	7	18	7	63.64	3	42.86	10	55.56
	1943	124	41	165	50	40.32	19	46.34	69	41.81
	1946	75	44	119	45	60.00	29	65.91	7[illegible]	62.18
	Total	266	121	387	129	48.50	66	54.55	195	50.39
Total		411	252	663	196	47.69	133	52.78	329	49.62

the size of their stopover range, or the readiness with which they enter traps and their tendency to become trap-shy or to acquire the trap habit after they are once trapped. If the factor of a bird becoming trap-shy or acquiring the trap habit can be disregarded (see pp. 417-418), then the greater length of stay in the fall than in the spring (Table 4) together with the fact that the percentage repeating is essentially the same in the two seasons, would indicate that the white-throat's stopover range is larger in the fall than in the spring.

LENGTH OF STAY AND NUMBER OF REPEATS

If a repeating bird is trapped over a period of several days, it can be assumed that its stay is at least these several days; if the bird's chance of getting trapped in a day is known, it is possible to estimate how much longer the bird stays without getting trapped. This chance is discussed further on p. 418.

While the non-repeating birds may have stayed only one day, two features of the data indicate that most of them probably stayed longer. A great many birds (Tables 2 and 3, especially the birds repeating only once) did not repeat for several days after they were first trapped; if these birds had not been trapped the second time it might have been assumed that they had left after their first capture. The varying lapse of time between successive captures of different birds suggests that there is considerable variation in the relation between the trapping area and the stopover ranges of different birds. Apparently some birds (e.g., those which stayed for several days before being retrapped) spent a part of their stay somewhere else besides near the traps. A second point which suggests that many non-repeating birds stayed more than one day is the distribution of the totals on the right hand side of Tables 2 and 3. Of the repeating birds, 6 out of 134 in the spring (4.48%) and 9 out of 195 in the fall (4.62%) showed a stay of only one day. If approximately half of *all* the birds stayed only one day (the 51.45% in the spring and the 49.61% in the fall which did not repeat), it would seem that more than four or five percent of the *repeating* birds would show a stay of only one day. It seems probable, therefore, that many of the birds which were trapped only once actually stayed more than one day, but spent the rest of their stay away from the traps; the average length of stay of the repeating birds is thus a better measure than an average based on all birds (assuming non-repeaters to stay only one day).

The data in Tables 2 and 3 show that in general the longer a bird stays the more times it is trapped. Correlation tests run with the data in these tables gave a correlation coefficient of 0.750 for the spring and 0.610 for the fall. These coefficients are highly significant, but their significance is somewhat impaired by the skewed distribution of the numbers of birds repeating different numbers of times (the totals at the bottom of the tables). To get around this, the data were grouped into contingency tables (a 4-by-4 table for the spring data and a 4-by-5 table for the fall data) and tested for association between length

TABLE 2. Summary of repeat and length of stay data on birds repeating in the spring. (The numbers in the table are numbers of repeating birds.)

Stay in Days	Number of Repeats																	Total	Aver. No. of Captures per Day
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	16	21	26		
1...........	6																	6	2.00
2...........	18	3	2		1													24	1.23
3...........	9	9	3	1														22	0.94
4...........	5	6	7	2														20	0.83
5...........	2	2	2	1	1	3	1					1						13	1.09
6...........	2	2					1	1										6	0.75
7...........	1	3	1	1	1		2	2										11	0.78
8...........		1	1	6		1	1							1				11	0.76
9...........	1	1	1				1	1			1		1					7	0.83
10...........							1											1	0.80
11...........							1							1				2	1.05
12...........							2	1		1								4	0.75
13...........									1				1		1			3	1.03
14...........												1				1		2	1.25
15...........											1						1	2	1.30
Total.......	44	27	17	11	3	4	10	5	1	1	2	2	2	2	1	1	1	134	
Aver. No. of Captures per Day	0.69	0.69	0.91	0.77	1.29	1.22	0.92	1.10	0.77	0.92	1.00	1.37	1.27	1.58	1.31	1.57	1.80		0.93

of stay and number of repeats; the chi square values so obtained were highly significant.

The data in Table 4 show that there is no significant difference between adults and immatures in the number of times they repeat or in their length of stay, and that there is no significant differences between the spring and fall in the number of times the birds repeat. The averages in the table are given plus or minus the standard error, s_x. The different length of stay in the spring and fall is highly significant; repeating birds stay longer in the fall than in the spring.

While the white-throats stayed longer in the fall than in the spring, they were trapped less frequently in the fall. The repeating birds averaged 0.93 captures per day in the spring, as compared with 0.48 captures per day in the fall. These figures are based on eight spring and fall seasons; the last column in Table 7 gives the average number of captures per day in seven different seasons. This difference in capture frequency indicates that either the traps were less attractive to the birds in the fall (perhaps because of the greater availability of food elsewhere), or that the birds had a larger stopover range in the fall.

Table 4 shows that there has been some variation from year to year in both the average number of repeats per bird and the average length of stay. It is to be expected that the species' migratory behavior would vary somewhat from year to year, as the various factors which might influence migration (weather conditions, food supply, etc.) are never exactly the same in successive years.

THE CHANCE OF A BIRD'S BEING TRAPPED

In order to attack the problem of the numbers of white-throats, it is necessary to know something of a bird's chance of being trapped, and if this chance is the same for all birds, and if it is influenced by the number of times the bird has been previously trapped. A basic assumption that is made in the discussion of numbers is that banded and unbanded birds have equal chances of being trapped; while this may seem to be a safe assumption, it may be that a bird once trapped may become trap-shy and be less likely to be retrapped, or a bird once trapped may acquire the trap habit and be more likely to be retrapped.

The probability of a bird's being trapped in a day, p, may be calculated by either of three methods: (1) Since there is a correlation between a bird's length of stay and the number of times it is trapped (see p. 416), p may be calculated as the average num-

TABLE 3. Summary of repeat and length of stay data on birds repeating in the fall. (The numbers in the table are numbers of repeating birds.)

Stay in Days	Number of Repeats																		Total	Av. No. of Captures Per Day
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	25	32	35		
1	9																		9	2.00
2	16	1																	17	1.03
3	18	5	3	1															27	0.84
4	10	5	3																18	0.65
5	7	1	1	1															10	0.52
6	3	2		1															6	0.47
7	5	2	1																8	0.36
8	7	7	3	2					1										20	0.42
9	5	4		2									1						12	0.43
10	3	1	1		1														6	0.32
11	2	6	5										1						14	0.36
12	2	3	1			1													7	0.29
13	3	1														1			5	0.54
14				1	1						1								3	0.55
15	1	1			1		2	1											6	0.40
16	1	1	1	1	1			1					1						7	0.38
17						1													1	0.41
18						1	1												2	0.42
19										1									1	0.58
20															1				1	0.75
21			1			1		2	1										5	0.37
22														1					1	0.68
23					1													1	2	0.91
24					1														1	0.25
27			1																1	0.15
29												1		1					2	0.48
31				1															1	0.16
34					1														1	0.18
38																	1		1	0.87
Total	92	40	21	10	7	4	3	4	2	1	1	1	3	2	1	1	1	1	195	
Av. No. of Captures Per Day	0.39	0.38	0.42	0.64	0.31	0.41	0.50	0.49	0.69	0.58	0.86	0.45	1.17	0.59	0.75	2.00	0.87	1.57		0.48

TABLE 4. Summary by seasons of the number of repeats and length of stay made by repeating birds.

Season		Number of Repeats						Length of Stay (in Days)					
		Adults		Immatures		All Repeating Birds		Adults		Immatures		All Repeating Birds	
		Max.	Average	Max.	Average	Max.	Average	Max.	Average	Max.	Average	Max.	Average
Spring	1939	7	3.3±1.9	3	2.0±1.0	7	2.8±1.1	9	5.3±1.9	8	5.5±2.5	9	5.4±1.3
	1940	21	4.1±1.3	26	4.5±2.0	26	4.3±1.1	15	6.4±1.0	15	5.5±1.3	15	6.0±0.9
	1941	7	3.7±1.8	6	3.7±1.5	7	3.7±1.0	11	7.0±2.1	8	6.7±0.9	11	6.8±1.0
	1942	–		2	2.0	2	2.0	–		4	4.0	4	4.0
	1943	3	1.4±0.3	12	4.0±1.1	12	3.0±0.7	7	3.0±0.7	14	5.4±1.0	14	4.5±0.7
	1944	8	3.4±0.5	16	6.5±1.4	16	4.7±0.2	9	4.4±0.5	13	5.5±0.3	13	4.8±0.2
	1946	1	1.0	3	2.0±1.0	3	1.5±0.5	9	5.0±4.0	3	2.5±0.5	9	3.8±1.8
	1947	14	5.1±1.1	9	3.1±0.5	14	4.0±0.6	13	6.2±0.9	13	4.7±0.7	13	5.4±0.5
	Total...	21	3.7±0.5	26	4.1±0.5	26	3.9±0.4	15	5.4±0.4	15	5.1±0.4	15	5.3±0.3
Fall	1938	4	2.8±0.5	3	1.7±0.3	4	2.0±0.3	3	2.8±0.3	16	4.9±1.5	16	4.3±1.1
	1939	35	11.8±4.4	2	2.0	35	9.7±4.0	23	10.4±2.3	3	3.0	23	9.6±2.2
	1940	14	5.1±1.3	5	2.5±0.9	14	4.6±1.1	29	10.8±2.2	24	13.8±3.6	29	11.4±1.8
	1941	15	5.6±2.4	5	3.3±1.2	15	4.9±1.7	31	16.1±3.7	34	14.7±9.7	34	15.7±3.1
	1943	9	1.9±0.2	5	1.7±0.3	9	1.9±0.2	16	6.3±0.5	23	6.5±1.3	23	6.3±0.5
	1946	10	2.6±0.4	32	3.6±1.1	32	3.0±0.5	19	9.1±0.8	38	11.1±1.7	38	9.9±0.8
	Total...	35	3.4±0.4	32	2.7±0.5	35	3.1±0.3	31	8.5±0.5	38	9.1±1.0	38	8.7±0.5
Total...........		35	3.5±0.3	32	3.4±0.4	35	3.5±0.2	31	7.4±0.4	38	7.1±0.6	38	7.3±0.3

ber of captures per day of the repeating birds. The values of p obtained by this method for seven different seasons are given in Table 7. (2) When estimates have been obtained of the numbers of birds present at the banding station each day during the season, p may be calculated as the average proportion of the birds present each day that were trapped. This method is discussed further on page 420, and the p values obtained are given in Table 7. (3) Values of p may be calculated from the formula ${}_{d}p_{n} = {}_{d}C_{n}p^{n}(1-p)^{d-n}$ as described on page 426. This is a less reliable method of estimating p, but the results obtained are of some interest. Using this method, p values are obtained for birds trapped on different number of days; these values are given in Tables 5 and 10.

TABLE 5. Table of p values (where p = the probability of a bird being trapped in a day), based on the formula for the probability of a bird staying d days being trapped on n different days: ${}_{d}C_{n}p^{n}(1-p)^{d-n}$

Based on Birds Trapped on:	Spring	Fall
1 or 2 different days.........	.2325	.1632
2 or 3 different days.........	.4792	.2469
3 or 4 different days.........	.5992	.2139
4 or 5 different days.........	.4892	.3313
5 or 6 different days.........	.4565	.2177

While these three methods give different values for p, it is significant that they all give higher values for p in the spring than in the fall. Apparently a bird's chance of being trapped in a day is greater in the spring than in the fall. This indicates (1) that a greater percentage of the birds passing through the station were caught in the spring than in the fall, (2) that the observed length of stay is probably nearer the actual length of stay in the spring than in the fall, (3) that the birds stay closer to the traps in the spring than in the fall (i.e., the stopover range is smaller in the spring), and (4) that the traps are more attractive to white-throats in the spring than in the fall (perhaps because other food is more scarce in the spring).

Of the three methods of determining p, the first method is probably the most reliable, and it is also the simplest method. Being the observed frequency of capture of the repeating birds, it certainly represents the average chance of *these* birds' being trapped in a day.

It is apparent from Tables 2 and 3 that there is considerable variation in the frequency of capture of different birds (and hence in p), both among birds captured the same number of times (the columns in the tables), and among birds staying the same length of time (the lines in the tables). This variation is probably due to differences in the stopover ranges of different birds; e.g., a bird trapped only twice in 16 days (Table 3) must have spent most of its stopover somewhere else beside near the traps, while one trapped 14 times in 16 days must have spent most of its stopover in the vicinity of the traps.

The question of whether a bird's chance of being trapped is influenced by previous trapping, i.e., whether white-throats become trap-shy or acquire the trap habit, may be approached by three different methods.

(1) If the probability of a bird being trapped was constant, regardless of the number of times it had been trapped previously, then the numbers of birds trapped different numbers of times would follow the

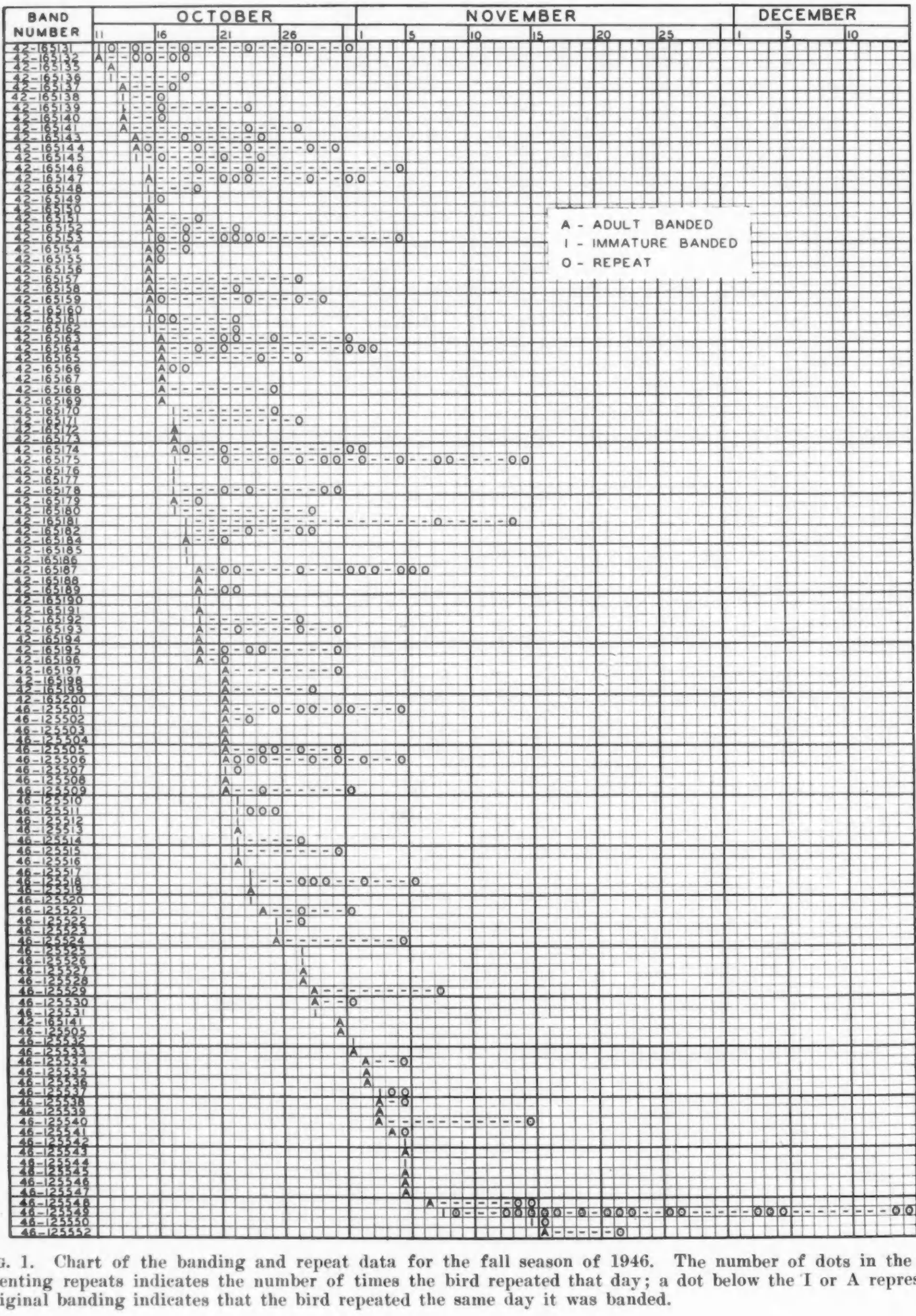

FIG. 1. Chart of the banding and repeat data for the fall season of 1946. The number of dots in the circles representing repeats indicates the number of times the bird repeated that day; a dot below the I or A representing the original banding indicates that the bird repeated the same day it was banded.

Poisson distribution. This distribution can be expressed by the equation, $y = \frac{nm^x}{x! : e^m}$, where y = the number of birds, x = the number of repeats, n = the number of birds banded, m = the average number of repeats per bird banded, and e = the base of natural logarithms (approximately 2.71828). Figure 2 shows the numbers of birds captured different numbers of times, along with the curve of the Poisson distribution, for the spring and fall seasons. It is obvious from this figure that the numbers of birds trapped different numbers of times do not follow the Poisson distribution (this disagreement is also shown by a chi square test for fitness); the observed numbers are in excess of the Poisson at either end, and are less than the Poisson in the central portion of the range. It is interesting to note that the graphs are similar for both the spring and fall data.

The fact that more birds fail to repeat than would be expected in the Poisson distribution may be due to one or more of three factors: (1) these birds stayed only a short time and did not have time to repeat, (2) the trapping station was located at the periphery of the stopover range of these birds and most of their stay was spent in other parts of this range, or (3) these birds became trap-shy. Since many non-repeating birds probably stayed more than one day (p. 414), the first factor is probably not the important one. While the second factor probably enters the picture, the similarity of the spring and fall graphs (Fig. 2), in spite of the fact that the stopover range is probably larger in the fall than in the spring, suggests that this factor is at least not the sole one. This leads to the conclusion that some birds become trap-shy.

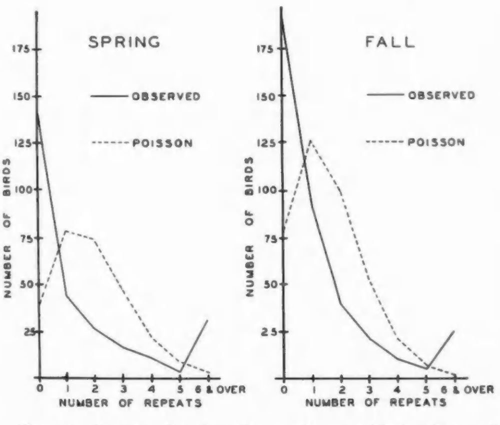

FIG. 2. Graphs showing the number of birds observed to repeat different numbers of times (solid line), compared with the numbers that should have repeated different numbers of times if the probability of a bird being trapped was constant, regardless of the number of times it had been trapped previously (broken line: Poisson distribution). The curve representing the Poisson distribution is based on the formula $y = \frac{nm^x}{x! \cdot e^m}$, where the value of m is derived from the observed data; for the spring m = 1.899, and for the fall m = 1.581.

(2) The number of captures per day of the repeating birds, which is a measure of p, is not the same for birds caught different numbers of times (see the bottom line of Tables 2 and 3). It will be noted that these figures tend to increase as one goes to the right along the line, particularly in Table 2. This means that there is a tendency, which is more pronounced in the spring than in the fall, for birds trapped many times to be trapped more frequently (i.e., average more captures per day) than those trapped only a few times.

(3) The values of p obtained by the third method (Table 5) are somewhat higher for birds captured on two or more different days (the last four lines in the table) than for birds captured on only one or two days. While this method of calculating p is probably not too reliable, it is interesting to note that the results obtained indicate that a bird trapped on only one or two days has less chance of being trapped in a day than one trapped on several different days.

The data from all three of these methods show that birds trapped several times have a greater chance of being retrapped than birds trapped only a few times. This indicates that some birds acquire the trap habit. The greater tendency for white-throats to acquire the trap habit in the spring, shown particularly by the second method, may be the result of a smaller stopover range in that season, and/or the fact that the food in the traps is more attractive to the white-throats in the spring than in the fall.

The basic assumption that banded and unbanded birds have equal chances of being trapped is probably not entirely valid; some birds apparently become trap-shy after they are once trapped, and a few tend to acquire the trap habit. However, the numbers in these two groups may more or less cancel out, and in terms of all the birds this assumption may be a reasonable one. If this assumption is made, then we can go ahead with the problem of white-throat numbers.

NUMBERS OF WHITE-THROATS

In problems of determining animal populations, few workers have used the recapture data of marked individuals. Most discussions of population measurement techniques have been concerned with various methods of sampling or counting; in two recent summaries of bird population measurement (Lack 1937, Kendeigh 1944) the use of banding data to measure bird populations is given little more than passing mention, and in most textbook discussions (e.g., Hickey 1943, Pettingill 1946) it is not even mentioned. However, this method has been used with some success in the measurement of populations of various insects (Jackson 1936a, 1936b, 1939; Dowdeswell, Fisher, & Ford 1940; Fisher & Ford 1947), fish (Schnabel 1938, Underhill 1941), mammals (Green & Evans 1940, Dice 1941, Stickel 1946), and other animals.

Estimating the size of animal populations on the basis of recaptures of marked individuals involves the use of the following ratio, or some modification of it:

$$\frac{\text{total marked}}{\text{total population}} = \frac{\text{marked individuals recaptured}}{\text{total captured}}$$

or,

$$\text{total population} = \frac{\text{total marked X total captured}}{\text{marked individuals recaptured}}$$

This is referred to as the "Lincoln Index" (Lincoln 1930, Jackson 1936a, Leopold 1936, *et al.*), the "recovery index" (Jackson 1936a), and the "Peterson Method" (C. G. J. Peterson: Rept. Dansk Biol. Sta., 6:21; 1895).

This ratio simply states that marked individuals will be recaptured in proportion to their abundance in the total population; it assumes that the population remains constant and that the sampling is random. Where there are changes in the population during the sampling period, due to individuals moving into or out of the sampling area, or due to reproduction and/or deaths, the ratio must be modified to take these changes into account. This has been done by Jackson (1936b, 1939) in estimating populations of tsetse flies; Fisher and Ford (1947), in measuring populations of an arctiid moth, take mortality into consideration but not emergence. The probable error due to chance variations in the samples may be estimated by various statistical procedures, and it may be reduced by increasing the size of the samples or by increasing their number. These methods are discussed by Jackson (1936b, 1939), Schnabel (1938), and Underhill (1941). Whether or not the sampling is random is perhaps always a debatable point.

In the case of the white-throat, where we are concerned with the numbers of transient individuals in a given small area, it is obvious that the number of individuals in the area will change from time to time, mainly on account of arrivals and departures. However, let us consider two aspects of the problem of white-throat numbers: (1) the daily populations of the species in the area of the banding station, and (2) the total number of individuals which pass through the station in a given season. The number of birds trapped daily, or in a given season, is a known quantity; the problem is to estimate the number of birds that are not trapped.

DAILY POPULATIONS

Once the banding and repeat data for a given season have been charted as in Figure 1, certain counts can be made for each day:

U = the number of unbanded birds trapped (which are banded and released).

B = the number of banded birds trapped (birds repeating).

C = the total number of birds trapped (C = U + B).

A = the number of banded birds not trapped, but assumed to be present in the area; these are birds trapped both before and after the day in question (the dashes in Figure 1).

K = the total number of birds known to be present (K = C + A).

Of these figures, K is nearest to N (the actual total number of birds present on the day in question). During the height of the migration, when some new birds are trapped practically every day, there are probably more than K birds present; during the latter part of the season, when no new birds are trapped, K is probably very close to N, if not actually equal to it.

There are two methods by which the daily values of N can be estimated from the repeat data; the estimates obtained by these methods can be referred to as N_1 and N_2, respectively.

Method 1. At the end of a given day of trapping, n_1, a certain number of banded birds (Kn_1) and probably some unbanded birds are present in the area. If it is assumed that the same birds are present the next day (n_2), and that both banded and unbanded birds have equal chances of being trapped, then the Lincoln Index ratio can be used to determine the population these two days (n_1 and n_2):

$$\frac{Kn_1}{N_1(n_1 \text{ and } n_2)} = \frac{Bn_2}{Cn_2} \text{ or } N_1(n_1 \text{ and } n_2) = \frac{Kn_1 \times Cn_2}{Bn_2}$$

The assumption that the same birds are present on two successive days is not necessarily valid; the population may change from one day to the next due to arrivals and departures. This method is therefore subject to error on account of such changes in the population. Another sources of error lies in the variations due to chance in the small samples involved. To partly correct for these sources of error, N_1 may be calculated for various two-day periods, e.g., n_1 and n_2, n_2 and n_3, n_3 and n_4, etc., and the estimate of N_1 for any day n_x can be taken as the average of the two values calculated for that day:

$$N_1 n_x = \tfrac{1}{2}\left[\frac{Kn_{x-1} \times Cn_x}{Bn_x} + \frac{Kn_x \times Cn_{x+1}}{Bn_{x+1}}\right]$$

Jackson's method (1939) of estimating populations from the recaptures of marked individuals might seem particularly applicable to white-throat data, since it allows for a regular turnover of the population. With such a turnover, the proportion of marked individuals in the population will decline in a geometric progression; by noting the proportion of marked individuals in the catch in several subsequent recapture periods, Jackson determined the nature of this geometric progression and then by extrapolation determined the proportion of marked individuals present the day of marking; then he used the Lincoln Index ratio to estimate the population that day. The calculations involved in determining populations by this method are rather laborious, and the reader is referred to Jackson's paper for a description of the method. The writer has used this method to estimate daily populations for the fall season of 1946, but the figures obtained were very erratic. Jackson worked with tsetse flies, and dealt with much larger numbers of individuals than are involved in these data on the white-throat. The inadequacy of this method when applied to the writer's data is apparently due to the small size of the samples, and the erratic figures obtained are due to chance variations in the samples.

Method 2. If both banded and unbanded birds

have equal chances of being trapped, then on any given day equal proportions of the banded and unbanded birds present should be trapped. That is, for any day:

$$\frac{\text{the number of banded birds trapped}}{\text{the number of banded birds present}} = \frac{\text{the number of unbanded birds trapped}}{\text{the number of unbanded birds present}} = \frac{\text{the total number of birds trapped}}{\text{the total number of birds present}}$$

$$\text{or, } \frac{B}{A+B} = \frac{U}{N-(A+B)} = \frac{C}{N}$$

Since all these values except N are known, we can solve for N (N_2):

$$N_2 = \frac{C(A+B)}{B}$$

This method is subject to error because of the fact that the value A + B may be larger than the banding data would indicate, as some banded birds not trapped on or after a given day may actually be present that day; this error is probably less in the spring than in the fall (see p. 424). The ratio B/ (A + B) is thus a maximum, and N_2 a minimum. The principal source of error, however, lies in the fact that the numbers of birds involved are small, and variations due to chance have considerable effect on the calculated estimates of N.

Of these two methods of estimating N the second method is probably better, particularly if the number of birds handled daily is not too small, as it is based on assumptions that appear more valid than those on which the first method is based. The second method has one disadvantage: no estimates can be made for days on which no banded birds were trapped. Because of the small numbers of birds involved neither method is very accurate, as may be shown by calculations of the standard error of proportion. The standard error of proportion, s_p, is calculated from the formula $s_p = \sqrt{\frac{p(1-p)}{A+B}}$, where p is the proportion

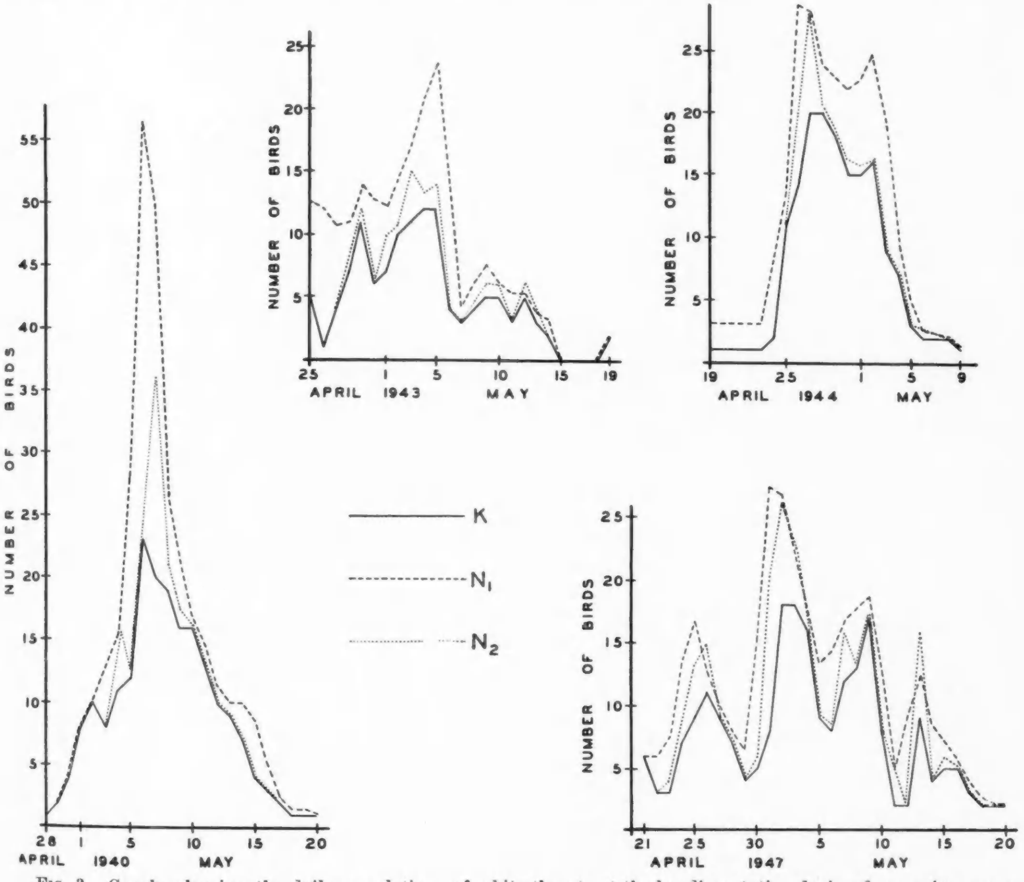

FIG. 3. Graphs showing the daily populations of white-throats at the banding station during four spring seasons. Solid lines, K (number of birds known to be present); broken lines, N_1 (number estimated by Method 1); dotted lines, N_2 (number estimated by Method 2).

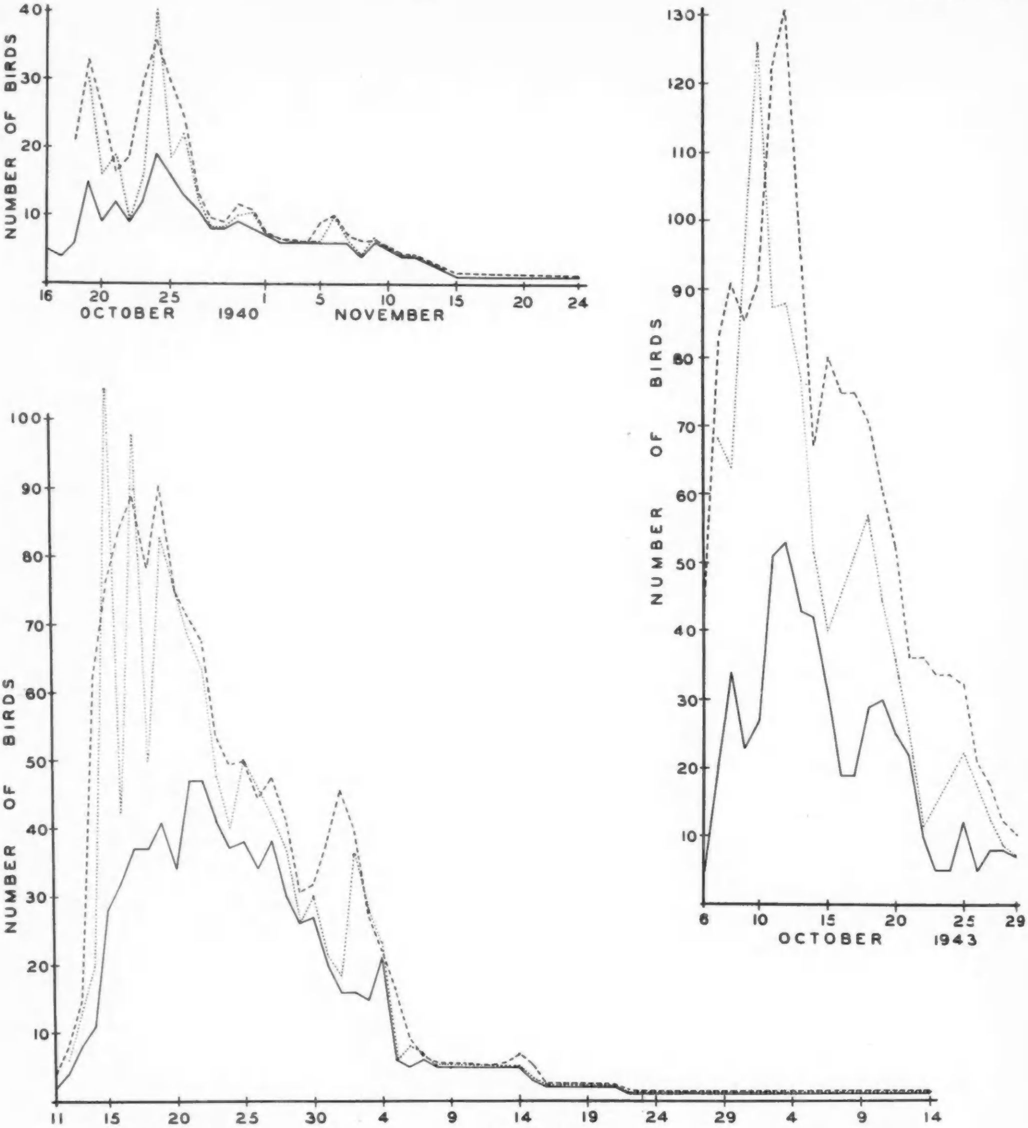

FIG. 4. Graphs showing the daily populations of white-throats at the banding station during three fall seasons. Solid lines, K (number of birds known to be present); broken lines, N_1 (number estimated by Method 1); dotted lines, N_2 (number estimated by Method 2).

of the banded birds present on a given day which are trapped that day, and A + B is the total number of banded birds known to be present that day. If p is not too close to zero or one, and the value of A + B is large, the 95% fiducial limits of p are $p \pm 1.96s_p$; 1.96 is the value of $t_{.05}$ with an infinite number of degrees of freedom.

The banding data for the 1946 fall season, with daily populations estimated by the two methods just described, are given in Table 6. Daily populations for this season are shown graphically in Figure 4, along with siimlar data for two other fall seasons, and the daily populations during four spring seasons are shown graphically in Figure 3.

It is interesting to note that the curve representing the number of birds known to be present (K, the solid line) parallels pretty well the curves representing the two methods of estimate (the dotted and broken lines), particularly in the spring. Thus, in the spring at least, the trend in K is a good index of

TABLE 6. Banding data and estimates of daily populations for the fall season of 1946. (The traps were not in operation on the dates starred.)

Date	Banding Data					Estimates of Daily Populations			
	U	B	C	A	K	N_1	C/N_1	N_2	C/N_2
10-11	2	0	2	0	2	4.0	.50	...	—
10-12	2	1	3	1	4	8.0	.38	6.0	.50
10-13	5	0	5	3	8	15.0	.33	...	—
10-14	3	2	5	6	11	62.3	.08	20.0	.25
10-15	17	2	19	9	28	76.1	.25	104.5	.18
10-16	7	10	17	15	32	83.8	.20	42.5	.40
10-17	11	4	15	22	37	88.8	.17	97.5	.15
10-18	5	9	14	23	37	78.1	.18	49.8	.28
10-19	10	6	16	25	41	90.3	.18	82.7	.19
10-20*	0	0	0	34	34	75.0	—	....	—
10-21	13	13	26	21	47	71.2	.37	68.0	.38
10-22	7	12	19	28	47	67.4	.28	63.3	.30
10-23	4	14	18	23	41	53.5	.34	47.6	.38
10-24	1	9	10	27	37	49.2	.20	40.0	.25
10-25	3	7	10	28	38	49.9	.20	50.0	.20
10-26*	0	0	0	34	34	44.5	—	....	—
10-27	4	17	21	17	38	47.1	.45	42.0	.50
10-28	3	8	11	19	30	41.1	.27	37.1	.30
10-29	0	4	4	22	26	30.6	.13	26.0	.15
10-30	2	10	12	15	27	31.8	.38	30.0	.40
10-31	2	10	12	8	20	37.6	.32	21.6	.56
11-1	3	7	10	6	16	45.4	.22	18.6	.54
11-2	4	2	6	10	16	40.0	.15	36.0	.17
11-3	1	1	2	13	15	27.6	.07	28.0	.07
11-4	6	11	17	4	21	22.1	.77	23.2	.73
11-5	0	2	2	4	6	16.5	.12	6.0	.33
11-6	1	1	2	3	5	9.3	.21	8.0	.25
11-7	1	3	4	2	6	6.3	.63	6.7	.60
11-8	0	2	2	3	5	5.5	.36	5.0	.40
11-9*	0	0	0	5	5	5.5	—	...	—
11-10*	0	0	0	5	5	5.5	—	...	—
11-11*	0	0	0	5	5	5.0	—	...	—
11-12	0	1	1	4	5	5.0	.20	5.0	.20
11-13	0	4	4	1	5	5.6	.71	5.0	.80
11-14	1	4	5	0	5	6.9	.73	5.0	1.00
11-15	1	2	3	0	3	5.3	.57	3.0	1.00
11-16	0	1	1	1	2	2.5	.40	2.0	.50
11-17	0	0	0	2	2	2.0	.00	...	—
11-18	0	1	1	1	2	2.0	.50	2.0	.50
11-19	0	0	0	2	2	2.0	.00	2.0	.00
11-20	0	1	1	1	2	2.0	.50	2.0	.50
11-21	0	2	2	0	2	2.0	1.00	2.0	1.00
11-22	0	1	1	0	1	1.5	.67	1.0	1.00
11-23*	0	0	0	1	1	1.0	—	...	—
11-24*	0	0	0	1	1	1.0	—	...	—
11-25	0	1	1	0	1	1.0	1.00	1.0	1.00
11-26	0	1	1	0	1	1.0	1.00	1.0	1.00
11-27	0	0	0	1	1	1.0	.00	...	—
11-28*	0	0	0	1	1	1.0	—	...	—
11-29*	0	0	0	1	1	1.0	—	...	—
11-30*	0	0	0	1	1	1.0	—	...	—
12-1*	0	0	0	1	1	1.0	—	...	—
12-2	0	1	1	0	1	1.0	1.00	1.0	1.00
12-3	0	1	1	0	1	1.0	1.00	1.0	1.00
12-4	0	1	1	0	1	1.0	1.00	1.0	1.00
12-5	0	0	0	1	1	1.0	.00	...	—
12-6	0	0	0	1	1	1.0	.00	...	—
12-7	0	0	0	1	1	1.0	.00	...	—
12-8	0	0	0	1	1	1.0	.00	...	—
12-9	0	0	0	1	1	1.0	.00	...	—
12-10	0	0	0	1	1	1.0	.00	...	—
12-11	0	0	0	1	1	1.0	.00	...	—
12-12	0	0	0	1	1	1.0	.00	...	—
12-13	0	1	1	0	1	1.0	1.00	1.0	1.00
12-14	0	1	1	0	1	1.0	1.00	1.0	1.00
Total	119					1352.8			
Aver.							.38		.54

U - number of unbanded birds trapped.
B - number of banded birds trapped.
C - total number of birds trapped (C = U + B).
A - number of banded birds present but not trapped.
K - total number of birds known to be present (K = C + A).
N - estimated total number of birds actually present (N_1, the number estimated by method 1; N_2, the number estimated by method 2).

the trend of the actual population. The two methods of estimating the daily populations give similar results, except that the figures obtained by Method 1 are in general higher than those obtained by Method 2. K and N are essentially the same in the latter part of the season, but during the height of the season N is greater than K.

The graphs for the spring of 1940 indicate that there were no pronounced waves; the daily populations quickly rose to a maximum, and then fell off. In the spring of 1943 there was apparently a wave of migration the first week in May, with smaller waves the last week in April and the second week in May. In the spring of 1944 there was a second wave the first few days in May, but the peak of the migration was the last week in April. In the spring of 1947 there were four distinct waves of migration, with the largest one coming the first week in May. These four graphs indicate that for the area of the writer's banding station, the peak of the spring migration of white-throats is around the end of April and the first of May.

The fall migration is spread over a longer period than the spring migration, with one or two big waves at the beginning of the season, occasionally smaller waves about the middle of the season, then a slow departure. In the fall of 1940 there were two major waves early in the season (shown by K and the two estimates of N), and two smaller waves about the middle of the season (shown by the two estimates of N, but not by K). A somewhat similar migration is shown in the fall of 1943, though the migration that season was apparently faster and less spread out; this is further indicated by the average length of stay, 6.3 ± 0.5 days in the fall of 1943, as compared with an average of 8.7 ± 0.5 days for all fall seasons combined. There is less similarity between K and the two estimates of N for the fall of

1946 than for any of the other seasons; the main wave is shown a week or so earlier by the estimates than by K. Both K and the estimates show a smaller wave the first few days in November, 1946.

Except for the fall of 1943, the fall migration was characterized by a few individuals staying for two or more weeks after the bulk of the migrants had gone on; this feature was less in evidence in the spring migration. While no attempt has been made to correlate these population trends with weather conditions, it is very likely that this lingering in the fall is influenced by the weather.

SEASONAL TOTALS

The total number of birds banded in a given season represents one measure of the total number passing through, and such figures might be used to compare the migration in difference seasons, providing equal proportions of the total were banded each season. Most banders make comparisons on this basis, but it would be interesting to know how many birds migrate through the station area without being trapped. At many banding stations, including the one operated by the writer, trapping methods (and probably also the fraction of the total which is trapped) vary from season to season, and the totals banded in different seasons may not be comparable.

There are three methods by which the total number of birds passing through the banding station area in a season can be estimated; the total to be estimated may be represented by the symbol Ts.

Method 1. If the chances of a bird being trapped or not being trapped are known, then the number missed (and hence the total which pass through the station) can be estimated. The probability of a bird being trapped in a day (p) may be calculated by either of three methods (see also p. 420): (1) p may be calculated as the average number of captures per day of the repeating birds. (2) p may be calculated as the average of the daily C/N ratios. The C/N ratio for any day represents the proportion of the birds present that day which are trapped, and the average of these ratios will represent a bird's average chance of being trapped in a day. The value of p so obtained will vary, depending on how many C/N ratios are used in obtaining the average; on days when no banded birds were trapped N_2 cannot be estimated, and on days when no white-throats at all were trapped (as often happens toward the end of the season) the C/N_1 ratio will be zero but there will be no value for C/N_2. Thus the value of p based on N_1 will usually be lower than that based on N_2. No matter which method is used to estimate N, the C/N ratios will fluctuate much more during the last days of the season than during the height of the season; if the last days of the season are eliminated in calculating p, the values obtained from the two N estimates are more similar. A comparison of the p values obtained by these different methods is shown in Table 7. In most of the seasons in this table, the p values obtained by using only the C/N ratios for the height of the season lie between those obtained by using all the C/N_1 and the C/N_2 ratios; therefore we can use the p values based on all the C/N ratios to calculate Ts, and say that the actual seasonal total (as determined from p values calculated from C/N ratios) lies between the two estimates obtained by using the highest and lowest values of p. (3) p may be calculated from the formula $_dp_n = {}_dC_n p^n (1-p)^{d-n}$ (see pp. 425-426).

TABLE 7. Values of p calculated by different methods. p = average probability that a bird will be trapped in a day; N = estimated daily population (N_1, estimated by method 1; N_2, estimated by method 2); C = total number of birds trapped each day.

Season		N by Method 1		N by Method 2		Average No. of Captures per Day of Repeating Birds
		All C/N_1 Ratios	C/N_1 Ratios During Height of Season	All C/N_2 Ratios	C/N_2 Ratios During Height of Season	
Spring	1940	.4949	.4975	.7111	.6918	.8743
	1943	.4703	.4393	.6978	.6546	.8936
	1944	.4258	.5559	.7655	.7539	1.1862
	1947	.5017	.5017	.6657	.6657	.9220
Fall	1940	.2863	.3600	.4702	.3617	.4885
	1943	.2774	.2774	.4221	.3860	.4508
	1946	.3768	.3424	.5359	.3363	.4187

If p represents the probability that a bird will be caught in a day, 1-p represents the probability that it will not be caught in a day. If a bird is present n days, then $1 - (1\text{-}p)^n$ represents the probability that it will be caught at least once, and $(1\text{-}p)^n$ represents the probability that it will not be caught at all. Thus, of all the birds which are present for n days, on the average $(1\text{-}p)^n$ of them are missed, and $1 - (1\text{-}p)^n$ of them are caught.

With a value for p, and knowing how many of the repeating birds stayed 1, 2, 3, etc. days, the total number of birds in each length-of-stay group can be estimated as follows:

If Tn = the total number of birds that stayed n days, and Yn = the number of trapped (repeating) birds that stayed n days, then

$$Yn = Tn\left[1-(1-p)^n\right], \text{ or } Tn = \frac{Yn}{1-(1-p)^n}$$

Totaling the Tn values for the different length-of-stay groups gives a figure (represented by STn) which, since it is based on only the number of repeating birds, must be corrected to include all birds. If it is assumed that the non-repeating birds actually stayed as long as the repeating birds, then Ts (the seasonal total) can be calculated as follows:

$$\frac{Ts}{\text{total number of birds banded}} = \frac{STn}{\text{number of birds repeating}}$$

$$Ts = \frac{STn \times \text{total number of birds banded}}{\text{number of birds repeating}}$$

Using Method 1 of estimating the seasonal total, three different estimates will be obtained for each

season: (1) using the p value obtained as the average of all the daily C/N_1 ratios, (2) using the p value obtained as the average of all the daily C/N_2 ratios, and (3) using the p value obtained as the average number of captures per day of the repeating birds. The p values obtained by the use of the probability formula (Method 3 of determining p) have not been used to estimate Ts by Method 1.

This method of estimating the seasonal total is based on three assumptions: (1) that the birds passing through the station area stay different lengths of time, (2) that the probability of capture in a day is the same for all birds, and (3) that the non-repeating birds stay as long as the repeating birds; the accuracy of this method depends on the validity of the assumptions, and on sampling errors. The first assumption seems warranted by the length of stay data (Tables 2 and 3). The second assumption is not entirely valid (see pp. 413-414), as some birds apparently become trap-shy and a few acquire the trap habit; however, these trap-shy and trap-habit birds are scattered among the different length-of-stay groups, hence the use of an average p value to obtain a Tn value for each group may be a reasonable procedure. The reasoning back of the third assumption has been noted above.

Table 8 shows the estimation of Ts by this method for the fall season of 1946, using three different values of p.

TABLE 8. Estimation of the total number of birds passing through the banding station (Ts) in the fall season of 1946 (by method 1).

n	Yn	p=average of daily C/N values				p=captures per day of repeating birds	
		N_1: p=.3768		N_2: p=.5359			
		$(1-p)^n$	Tn	$(1-p)^n$	Tn	$(1-p)^n$	Tn
1	2	.6232	5.31	.4641	3.73	.5813	4.98
2	5	.3884	8.18	.2154	6.37	.3379	7.55
3	7	.2420	9.23	.1000	7.78	.1964	8.71
4	8	.1508	9.42	.0464	8.39	.1142	9.03
5	3	.0940	3.31	.0215	3.07	.0664	3.21
6	1	.0586	1.06	.0100	1.01	.0386	1.04
7	2	.0365	2.08	.0046	2.01	.0224	2.05
8	7	.0228	7.16	.0017	7.01	.0130	7.09
9	4	.0142	4.06	.0001	4.00	.0076	4.03
10	3	.0088	3.03	.0000	3.00	.0044	3.01
11	8	.0055	8.04	.0000	8.00	.0026	8.02
12	4	.0034	4.01	.0000	4.00	.0015	4.01
13	2	.0021	2.00	.0000	2.00	.0009	2.00
14	2	.0013	2.00	.0000	2.00	.0005	2.00
15	4	.0008	4.00	.0000	4.00	.0003	4.00
16	2	.0005	2.00	.0000	2.00	.0002	2.00
17	1	.0003	1.00	.0000	1.00	.0000	1.00
18	2	.0002	2.00	.0000	2.00	.0000	2.00
19	1	.0001	1.00	.0000	1.00	.0000	1.00
21	3	.0000	3.00	.0000	3.00	.0000	3.00
27	1	.0000	1.00	.0000	1.00	.0000	1.00
29	1	.0000	1.00	.0000	1.00	.0000	1.00
38	1	.0000	1.00	.0000	1.00	.0000	1.00
Total	74	STn = 84.91		STn = 78.37		STn = 82.74	
Ts			136.54		126.03		133.05

Method 2. If each bird during a given season stays, on the average, d days, then it will be included in d different N totals (where N represents a daily population estimate); therefore,

$$Ts = \frac{\text{sum of the N values}}{d}$$

The best estimate of d is the figure representing the average length of stay of the repeating birds (Table 4). The Ts values obtained by this method for several different seasons are given in Table 9.

This method is subject to error in that the N values used are estimates, and are obtained by what is probably the less satisfactory of the two methods of estimating N (there are usually a few days during the season when no N_2 value can be estimated, hence the N_1 values must be used in this calculation). The d value used is based on only the repeating birds, and may not represent the average length of stay of all birds. It will be noted in Table 9 that the Ts estimates obtained by this method are lower than the actual number of birds banded in two seasons (spring and fall of 1940); in these seasons either the actual average length of stay was less than that used in the calculation, or the daily population estimates (N) were too low, or both. The average stay of the repeating birds these two seasons was relatively high as compared with the average stay in other seasons (see Table 4).

TABLE 9. Summary of estimates on the total number of White-throated Sparrows passing through the station in a season (Ts).

Season		METHOD 1 Estimates of Ts Based on p Values Derived from:			METHOD 2	METHOD 3	Number of Birds Banded
		C/N_1	C/N_2	caps/day	$Ts = \frac{SN_1}{d}$	highest and lowest	
Spring	1940	61.7	57.5	55.7	53.0	79.4 56.6	55
	1943	61.4	52.6	49.7	49.5	93.7 49.0	49
	1944	55.6	47.1	46.0	52.7	55.8 46.3	46
	1947	70.7	66.1	64.1	64.7	81.0 64.1	64
Fall	1940	57.1	50.1	49.8	34.0	87.6 60.0	47
	1943	242.8	198.6	193.8	230.0	277.5 177.5	165
	1946	136.5	126.0	133.1	136.6	149.5 125.0	119

Method 3. This method merits some consideration although the results obtained by it are somewhat erratic. It is based on two assumptions, (1) that the probability of a bird being trapped in a day is con-

stant, and (2) that all birds stay the same number of days; the erratic results obtained suggest that one or both of these assumptions are not valid. The validity of the first assumption is questionable (see p. 417); the second assumption is obviously not valid (Tables 2 and 3), but assuming that *on the average* all birds stay a given number of days might appear to be a satisfactory basis for dodging the issue.

If these two assumptions are made, then

$$ {}^{d}p_n = {}^{d}C_n p^n (1-p)^{d-n}, \text{ where } {}^{d}C_n = \frac{d(d-1)(d-2)....(d-n+1)}{n!} \quad (1)$$

In this formula, ${}^{d}p_n$ is the probability of a bird being trapped on n different days out of the d days it stays, p is the probability of a bird being trapped in a day, d is the length of stay in days, and n is the number of different days on which a bird is trapped. If N_n represents the number of birds which are trapped on n different days, then

$$\frac{N_1}{N_0} = \frac{{}^{d}p_1}{{}^{d}p_0} = \frac{dp(1-p)^{d-1}}{d(1-p)} = \frac{dp}{1-p} \quad (2)$$

$$\frac{N_2}{N_1} = \frac{{}^{d}p_2}{{}^{d}p_1} = \frac{\frac{1}{2}d(d-1)p^2(1-p)^{d-2}}{dp(1-p)^{d-1}} = \frac{p(d-1)}{2(1-p)} \quad (3)$$

Similarly,

$$\frac{N_3}{N_2} = \frac{p(d-2)}{3(1-p)} \quad (4)$$

$$\frac{N_4}{N_3} = \frac{p(d-3)}{4(1-p)} \quad (5)$$

etc.

Using any two of the above equations after (2), one can solve for d or p, since the N values are known, and with these values of d and p equation (2) can be used to calculate N_0 (the number of birds not trapped); adding N_0 to the number of birds banded gives the seasonal total Ts.

Using the N data for any given season, the values of d calculated from different pairs of equations do not agree; obviously this method cannot be used to determine d. If one takes as d the average length of stay of all repeating birds and then solves for p, the p values obtained using different equations are more similar, but not similar enough for this to be a satisfactory method of determining p. If, instead of using as d the average length of stay of all repeating birds, one uses the average length of stay of just the birds involved in the equation, the p values obtained using different equations are more similar.

Table 10 summarizes the calculations of Ts by this method for seven seasons. For some seasons (e.g., the fall of 1946) this method gives fairly consistent results, and the figures obtained agree fairly well with those obtained by other methods. For other seasons, however, the figures obtained are not very consistent, and do not agree very well with those obtained by other methods. It may be concluded that this is not a satisfactory method of estimating Ts, although it is of interest because of the values of p it gives (Table 5).

Table 9 gives a summary of the calculations of Ts for seven seasons, using different methods of estimate. The best conclusions from these figures is that the actual season total probably lies somewhere between the highest and lowest estimates.

On the basis of the figures in Table 9 it appears that the number of birds passing through the banding station area in the spring varies less from year to year than the number passing through in the fall. From 50 to 65 or more birds pass through during the spring, and from about 50 to over 200 pass through in the fall. The fall migration at this station was much heavier in 1943 and 1946 than during any spring season the station has been in operation.

EARLY AND LATE MIGRANTS

While it can be said with certainty that a bird trapped early in the season is an early migrant (at least as far as this area is concerned), it can only be said that birds trapped later in the season are *probably* later migrants. This probability can be expressed in terms of the p values mentioned above: the probability of a bird being at the station n days before it is trapped is $(1\text{-}p)^n$. The value of $(1\text{-}p)^n$ becomes insignificant after a day or two in the spring, and after four or five days in the fall (Table 8). Thus the data on late arrivals in the spring probably refer to birds that actually arrive late, while the fall data on what appear to be late arrivals may in some cases refer to birds that arrived a few days earlier than the day on which they were first trapped. Any conclusions that may be drawn from the data regarding the comparative migratory behavior of

TABLE 10. Estimation of the total number of birds passing through the banding station in a season (Ts), by method 3.

Value	Calculated From		Spring				Fall		
	d_n, when n =	N_n, when n =	1940	1943	1944	1947	1940	1943	1946
N_n	—	1	28	30	17	26	28	100	47
	—	2	11	11	9	14	8	35	35
	—	3	5	1	7	8	4	20	13
	—	4	4	2	5	6	0	7	6
d	—	2	3.18	2.82	2.56	3.36	5.50	4.71	6.34
	—	2, 3	3.81	2.92	3.63	3.41	6.58	5.87	7.25
	—	3, 4	6.11	5.33	5.08	4.00	8.75	8.22	10.16
p	2	1, 2	.2649	.2872	.4043	.3136	.1127	.1587	.2181
	2, 3	2, 3	.4297	.2287	.5887	.5489	.2467	.3070	.1751
	3, 4	3, 4	.5071	.7744	.5787	.7500	.....	.2115	.2050
N_0	2	1, 2	24.43	26.40	9.78	16.95	40.09	112.53	26.58
	2, 3	2, 3	3.62	44.65	0.46	2.30	40.63	12.48	6.53
	3, 4	3, 4	1.63	0.002	0.25	0.07	.....	16.85	5.99
	2, 3	1, 2, 3	9.75	34.66	3.27	6.27	12.99	38.46	30.54
	3, 4	1, 3, 4	4.45	1.64	2.44	2.17	.....	45.36	17.94
Ts	2	1, 2	79.43	75.40	55.78	80.95	87.09	177.48	145.58
	2, 3	2, 3	58.62	93.65	46.46	66.30	87.63	181.85	125.53
	3, 4	3, 4	56.63	49.00	46.25	64.07	.....	203.46	124.99
	2, 3	1, 2, 3	64.75	83.66	49.27	70.27	59.99	277.53	149.54
	3, 4	1, 3, 4	59.45	50.64	48.44	66.17	.....	210.36	136.94

early arrivals as compared with late arrivals must be considered in the light of this possibility of error, particularly in the case of the fall migration.

Repeat data should throw some light on the problem of whether or not migration is of a "leap-frog" nature. There is evidence that in many species the first arrivals in the spring at a given point in the breeding range stop and take up nesting territories, while later arrivals continue on and nest farther north. Also, birds in their northward migration in the spring may pass through areas still occupied by wintering individuals of the same species, and these latter individuals may not start *their* northward migration until after many or all of the individuals that have wintered south of them have passed through. If this same type of behavior occurs on the migration route, it would mean that the early arrivals at a given stopover point on the route would remain until after later migrants had arrived and left. Leap-frog movement on the migration route would be indicated by the repeat data if it could be demonstrated that the early arrivals stayed longer than the later arrivals.

Table 11 gives a summary of the seasonal trend, by six-day periods, in the percentage of banded birds repeating and in the average length of stay of the repeating birds. These figures show that in general as the season advances the percentage of banded birds repeating and the length of stay tend to decrease. In some seasons, e.g., the fall of 1940 and the fall of 1946, the length of stay tends to increase again toward the latter part of the season. The abrupt rise in average length of stay in the fifth six-day period in the fall of 1946 was due mainly to one bird, No. 46-125549, which stayed 38 days; this bird was abnormal in that the upper mandible was bent to the left at almost a right angle.

Correlations were run on the length of stay and the day of the season on which the repeating bird was banded; the coefficients of correlation obtained showed a significant correlation in only two seasons, the spring of 1940 and 1944. In the case of the fall season of 1946, excluding the last four birds banded gave a significant correlation. It may be concluded that in some seasons the average length of stay decreases as the season advances, i.e., birds arriving early in the season stay longer than those arriving later. The percentage of banded birds repeating, which may serve as another measure of the speed with which the birds pass through the station, supports this conclusion.

TABLE 11. Percent of banded birds repeating, and average length of stay, of birds banded in successive six-day periods.

Six-day Period		Spring 1940*	Spring 1943	Spring 1944**	Spring 1947	Fall 1940	Fall 1943	Fall 1946†
1	% Rep.	57.14	55.00	100.00	66.67	48.83	60.56	80.56
	Aver. Stay	9.6	4.7	6.0	6.3	11.9	7.0	10.5
2	% Rep.	56.76	36.84	75.86	68.75	29.41	26.67	60.87
	Aver. Stay	4.8	4.4	5.2	6.5	12.0	6.3	10.3
3	% Rep.	0.00	33.00	40.00	78.57	50.00	28.57	46.67
	Aver. Stay	.....	4.5	3.2	3.0	8.0	5.1	7.4
4	% Rep.	0.00	50.00	.....	23.08	0.00	28.57	41.67
	Aver. Stay	.....	2.0	.....	7.3	.....	2.8	5.0
5	% Rep.	.....	0.00	.....	33.33	100.00	.....	25.00
	Aver. Stay	.....	.....	.....	3.0	9.0	.....	23.5
6	% Rep.	.....	.....	.....	.....	.....	.....	100.00
	Aver. Stay	.....	.....	.....	.....	.....	.....	4.5

*Correlation significant.
**Correlation highly significant.
†Correlation significant if the last four birds banded are omitted.

It thus appears that there is a certain amount of leap-frogging of white-throats along the migration route, particularly in the spring.

Another problem of migration on which repeat data should throw light, particularly if accompanied by recovery data, is the relative speed of migration of a bird in different parts of its migration route. It is believed that many species increase their speed of migration as they approach their breeding grounds in the spring; perhaps the same is true of southward migrants as they approach their wintering grounds in the fall. The length of a migrant's stay at a stopover point on its migration may serve as an index of its speed of migration. A difficulty of interpreting repeat data in the light of this problem lies in the absence of recovery records; without recoveries, we can never be sure where our birds are heading.

Since there is a tendency in the spring migration for the length of stay of migrating white-throats to decrease as the season advances, it may be said that the general speed of migration of the later migrants is greater than that of the earlier migrants. If the white-throat increases its speed of migration as it approaches its breeding grounds, it might be inferred that the birds which pass through this station late in the season are (while at the station) nearer their breeding grounds than the birds which arrive earlier in the season. Confirmation of this point, however, must await recovery at their breeding grounds of birds banded here in the spring.

The same thing might be inferred about the fall migrants, though with less assurance, as the correlation between length of stay and the day the bird is banded is less significant, and the birds not trapped until late in the season may not actually be late arrivals.

The data show that there is little difference in the proportions of adults and immatures at the station in different parts of the migration season, except in the 1943 fall season; in that season there was a relatively larger proportion of immatures during the first week of the season and a larger proportion of adults during the middle of the season. A wave of migrants that arrived on October 7 of that season consisted mostly of immatures. For the most part adult and immature white-throats migrate together, but occasionally migrating flocks may consist mainly of one age group.

STOPOVER RANGE

The migration of the individual white-throat consists of nocturnal flights of some distance, separated by stopovers of one or more days during which the bird feeds and rests before the next nocturnal flight. The length of these nocturnal flights can be determined only by the lucky capture of the same bird at separated localities on successive days. There appears to be only one such record for the white-throat (Fischer & Gill 1946, p. 410), indicating a nocturnal flight of 60 miles on a fall migration. The area over which an individual bird ranges during these stopovers, which may be called the *stopover range*, can be determined more easily than the length of the nocturnal flights, yet very little is known of this phase of migratory behavior. Most studies of bird migration have been concerned with other phases of the subject, and most studies of bird range or territory have been concerned with breeding or wintering birds. The problem of stopover range is a vital point in the analysis of repeat records, and it has been encountered repeatedly in this analysis. Because there is so little information on it for the white-throat, repeat data are often difficult to interpret. It is surprising that so little study has been made of this phase of bird migration.

While the size of the white-throat's stopover range might be determined by trapping (by using numerous traps strategically located over a sizable area), a better method would be by the use of colored bands or dyed feathers by which individual birds could be recognized in the field, coupled with extensive field observations. This latter method has been used to a limited extent by the writer, but the data so far obtained are insufficient to draw any definite conclusions. The location of the traps at the writer's station has been such that at best the size and nature of the white-throat's stopover range can only be estimated.

The traps at this station have varied in number and location in different seasons, but the most widely separated traps have usually been at least 100 yards apart, and in some seasons have been nearly 200 yards apart. Birds have frequently been caught in traps 100 yards apart (about 20 per cent of the repeating birds in the 1946 fall season were caught in traps 100 yards apart), but relatively few have been caught in traps farther apart than this. In the 1946 fall season the average distance between the most widely separated traps in which each of the 74 repeating birds was caught was 58.18 yards; this distance varied from zero (a bird repeating only in the same trap in which it was originally caught) to 125 yards.

During the seasons that this banding station has been in operation there have been no other banding stations nearer than about four miles, except for the 1939 fall season. During that season Mr. Robert Roswurm operated a banding station about one-fourth mile from the University Botanical Garden; one of his white-throats (an immature, No. 40-29770) was caught at the writer's station. This is the only white-throat banded by another bander that has ever been caught at the writer's station.

On the basis of trap capture data, it appears that the majority of the white-throats that stop over at this banding station probably do not range over more than eight or ten acres during their stay; many probably do not range over more than one or two acres, but some birds may range as far as one-fourth mile.

While it may not be possible to determine from the repeat records the exact size of the white-throat's stopover range in any given season, it can be said that this range is larger in the fall than in the spring. The percentage of the banded birds which repeat and the number of times they repeat are essentially the same in the spring and fall, but in the fall the birds stay longer and repeat less frequently (see Tables 4 and 7); these facts indicate that the birds stay closer to the traps in the spring than in the fall.

SUMMARY

Relatively little use has been made of the repeat records of banded birds, yet such records may yield information on several problems of bird migration. This paper is an attempt to point out what may be learned from the repeat records of a transient species, the white-throated sparrow, and is based on the repeats of 329 birds (49.62% of the total banded over a period of several years) at the writer's banding station in Columbus, Ohio.

Several types of traps have been used, but the most successful for white-throats have been funnel traps (cloverleaf, maze, and government sparrow traps).

White-throats have been banded at the writer's station during nine spring and six fall seasons. The numbers banded per season varied from 3 to 64 in the spring and from 12 to 165 in the fall. The percentage repeating each season varied from 0.00% (the season 3 were banded) to 65.22% in the spring (48.55% for all spring seasons), and from 40.43% to 75.00% in the fall (50.39% for all fall seasons). The percentage of birds repeating is essentially the same in the spring and fall, and in adults as compared with immatures.

The number of repeats made by individual birds varied from 1 to 26 in the spring and from 1 to 35 in the fall, with an average of 3.9 ± 0.4 repeats per repeating bird in the spring and 3.1 ± 0.3 in the fall; the difference in the average number of repeats per bird in the spring and fall is not significant. On the average, adults repeated about as many times as immatures (3.3 ± 0.3 for adults and 3.5 ± 0.4 for immatures).

The varying interval between successive captures of different birds, and the distribution of the lengths-of-stay of the repeating birds, suggest that most of the non-repeating birds probably stayed more than a day; the average stay of the repeating birds is thus a better measure than the average of all birds banded.

The maximum length of stay of a repeating bird was 15 days in the spring and 38 days in the fall. On the average, there was no significant difference in the stay of adults as compared with immatures, but

the birds stayed significantly longer in the fall than in the spring; the repeating birds stayed an average of 8.7 ± 0.5 days in the fall and 5.2 ± 0.1 days in the spring. In general, the longer a bird stayed the more times it was trapped. The repeating birds were trapped at more frequent intervals in the spring than in the fall: 0.94 times a day in the spring, on the average, and 0.48 times a day in the fall.

The variation from season to season in the average number of repeats per bird and in the length of stay indicates that the migratory behavior of the white-throat varies somewhat from season to season; this may be due to weather conditions, food supply, or other factors.

Three methods are described by which the probability of a bird's being trapped in a day may be calculated. These methods give different figures, but they agree in giving higher values for the spring than for the fall; apparently a bird's chance of being trapped in a day is greater in the spring than in the fall. The variations in the frequency of capture of different birds suggest that all birds do not have the same chance of being trapped in a day.

Three different analyses of the repeat data indicate that some birds become trap-shy and a few acquire the trap habit, hence the chance of a bird's being trapped in a day may be influenced by its previous trapping experience. A basic assumption that is made in the discussion of numbers—that banded and unbanded birds have equal chances of being trapped—may therefore not be entirely valid, but the numbers of birds becoming trap-shy and those acquiring the trap habit may more or less cancel out and in terms of all birds this assumption may be reasonable.

Two methods are described by which the number of white-throats present at the station each day can be estimated, and graphs are presented to show the daily populations (as determined by different methods) in four spring and three fall seasons. The two daily population estimates parallel pretty well the numbers of birds known to be present, and show similar trends through the season.

The daily population trend through the season varies somewhat in different seasons, and is somewhat different in the spring and fall. In the spring the population builds up rapidly at the beginning of the season and falls off rapidly at the end of the season; occasionally waves of migration are indicated by the daily population figures. In the fall the population builds up rapidly at the beginning of the season and falls off more gradually the latter part of the season; there are frequently one or two major waves in the early part of the season, and one or more smaller waves about the middle of the season. A few birds tend to linger for a longer period at the end of the season in the fall than in the spring. The migration is generally spread over a longer period in the fall than in the spring.

Three methods are described by which the total number of birds passing through the station in a season can be estimated. The different figures obtained by two of these methods for a given season are fairly similar; the third method gave rather erratic results and is not considered satisfactory. The estimates obtained for seven different seasons indicate that the number passing through in the spring varies less from year to year than in the fall; from 50 to 65 or more birds pass through during the spring, and from 50 to over 200 pass through during the fall.

In general, as the season advances the percentage of banded birds repeating and the length of stay of the repeating birds tend to decrease, hence there is apparently a certain amount of leap-frogging during migration, particularly in the spring. The decrease in length of stay in the spring as the season advances may indicate, if the white-throat's speed of migration increases as it approaches its breeding grounds, that the late arrivals will not nest as far north as the earlier arrivals.

There is little or no difference in the proportion of adults and immatures present in different parts of the migration season; adult and immature white-throats apparently migrate together, though occasionally flocks may consist largely of one age group.

The stopover range of the white-throat is a key problem in the analysis of repeat data, and one about which very little is known. Our data indicate that most white-throats probably range over only a few acres during their stopovers, though some may range as far as one-fourth mile. The stopover range is larger in the fall than in the spring.

This analysis has raised a number of questions that cannot be satisfactorily answered, and suggests problems that should be investigated further. By marking trapped birds in such a way that they can be recognized in the field, coupled with extensive field observations, it should be possible to get a much better idea of the individual birds' length of stay and the nature of their stopover range. In situations where this type of study is not practicable, traps may be so located as to give a better idea of the stopover range.

LITERATURE CITED

Commons, Marie A. 1938. The log of Tanager Hill. Baltimore. xviii + 244.

Dice, L. R. 1941. Methods for estimating populations of mammals. Jour. Wildlife Manag. **5:** 398-407.

Dowdeswell, W. H., R. A. Fisher, & E. B. Ford. 1940. The quantitative study of populations in the Lepidoptera. I. Polymmatus icarus Rott. Ann. Eugen. **10:** 123-136.

Fischer, R. B., & Geoffrey Gill. 1946. A cooperative study of the white-throated sparrow. Auk **63:** 402-418.

Fisher, R. A., & E. B. Ford. 1947. The spread of a gene in natural conditions in a colony of the moth Panaxia dominula L. Heredity **1:** 143-174.

Green, R. G., & C. A. Evans. 1940. Studies on a population cycle of snowshoe hares on the Lake Alexander area. I. Gross annual censuses, 1932-1939. Jour. Wildlife Manag. **2:** 220-238.

Hickey, Joseph J. 1943. A guide to bird watching. New York. xv + 262.

Jackson, C. H. N. 1936a. The use of the recovery index in estimating the true density of tsetse flies. Trans. Roy. Ent. Soc. London **84:** 530-532.

1936b. Some new methods in the study of Glossina morsitans. Proc. Zool. Soc. London **1936:** 811-896.

1939. The analysis of an animal population. Jour. Animal Ecol. **8:** 238-246.

Kendeigh, S. Charles. 1944. Measurement of bird populations. Ecol. Monog. **14:** 67-106.

Lack, David. 1937. A review of bird census work and bird population problems. Ibis (14) **1:** 369-395.

Leopold, Aldo. 1936. Game management. New York. xx + 481.

Lincoln, Frederick C. 1930. Calculating waterfowl abundance on the basis of banding returns. U. S. D. A. Circ. 118, pp. 1-4.

Middleton, Raymond J. 1939. Length of stay of migrating birds in southeastern Pennsylvania. Bird-Banding **1:** 148-149.

Miller, Alden H. 1946. A method of determining the age of live passerine birds. Bird-Banding **17:** 33-35.

Pettingill, Olin Sewall, Jr. 1946. A laboratory and field manual of ornithology. Minneapolis. vi + 248.

Schnabel, Z. E. 1938. The estimation of the total fish population in a lake. Amer. Math. Monthly **45:** 348-352.

Stickel, Lucille F. 1946. Experimental analysis of methods for measuring small mammal populations. Jour. Wildlife Manag. **10:** 150-159.

Underhill, A. Heaton. 1941. Estimation of a breeding population of chub suckers. Trans. Fifth N. Amer. Wildlife Conf. 251-256.

ECOLOGICAL NOTES ON THE INSECT POPULATION OF THE FLOWER HEADS OF BIDENS PILOSA

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ECOLOGICAL NOTES ON THE INSECT POPULATION OF THE FLOWER HEADS OF BIDENS PILOSA

INTRODUCTION

Below the frostline in Florida and Texas, and southward in all lands adjacent to the Carribean Sea, there grows a vigorous white-flowered species of *Bidens, B. pilosa* L (= *B. leucantha* L.). The plant has many common names: "Spanish Needles," "Shepherd's Needle," "Old Maid's Pins," "White Sticktight," "Beggar's Ticks," "Pitch-forks," etc.; all suggested by the vagrancy of its seeds, which attach themselves with the greatest readiness to woolen clothing. The seeds when ripe are hung out in loose clusters by the side of every well-trodden path in that frostless subtropical area. Each slender seed is armed with a pair of barbed spines. The barbs on the spines face inward, as if to cooperate in hanging on to any wool into which they may be thrust, whether that wool be woven into garments or lie loosely on the back of an animal. So, the weed scatters its seeds, and gains wide distribution.

I have observed no insects feeding upon the mature seeds, though there may well be some that do; but I have been greatly interested in the large population of the flower heads that feeds on the seeds during their development, while they are still soft and edible. The continuing community so maintained is the subject of these notes.

This community was come upon almost by accident. While collecting dragonflies in the Florida Everglades, I noticed that a blossoming spray of Bidens at my feet had many imperfectly developed flower heads on it. I plucked one head and split it open with my pocket knife and found some insect galls in it. The galls were all in the outer florets of the head, and each gall was developed wholly in the corolla of a single flower. Among the many insect galls that I have seen in my time I had but once before seen one that was strictly a corolla gall; so that was interesting. A similar gall was found in heads of *Senecio douglassi* at Claremont, California, in December 1922.

I split open another head and found two fruit-fly puparia at the center of it. They were occupying cavities in the seed-layer of the head, where as larvae they had eaten out the developing seeds. I split other heads and found the larvae of very small moths, eating tunnels through the seed layer; then other larger caterpillars that were eating all the seeds of the head and boring down into the receptacle underneath them. Then I found the larvae and pupae of parasites that may have belonged with any of the foregoing seed-eaters; all in addition to the very minute thrips and mites, that are to be expected in flower heads generally.

It has long been known that the larvae of certain insects live in the seed layer of the heads of many Compositae and other head-bearing plants. When I began searching the heads of Bidens, I was at first merely interested in seeing how many kinds of insects I could find in them. Many kinds were present, though a single head could afford food and shelter for only a few. When opportunities came, I collected on visits to different places, and found the same resident species present in them all.

The study of this population was begun as a winter vacation pastime. It was continued with much more interest when I began to realize that here was a nomad community of insects whose members live together in relations of mutual adjustment, find both residence and food supply in Bidens flower heads, and make shift to follow in successive generations the successive opening of the flowers.

Most of the work hereinafter reported was done in the field with the use of a sharp pocket knife, a fine forceps and a 10x pocket lens. These appliances were used first to find what insects were present in the heads and where, and then to discover what each species was doing.

Only insects were studied; the mites often present were too small for the magnification and the equipment available. The ubiquitous thrips received scant notice. Hundreds of heads were opened and dissected for the resident insects, as a qualitative beginning. Thousands of clipped-off heads were kept in small glass rearing jars under weighted cheesecloth covers. Day by day as the insects emerged in the jars, they were preserved for future study. This was a sort of random census-taking. A good many larvae were isolated and reared in separate containers as a means of matching them with their adults.

I have published a short account of these insects for popular reading in the National Geographic Magazine for September (Vol. 90, 1946) under the title "A Community of Dwarfs," with illustrations in color from photographs that were made by Mr. Willard Culver. I wish here to give a more complete listing of the insects, with further ecological data concerning some of them.

Acknowledgment of aid lent me in the course of this study is due to a number of friends in Florida. While working in Englewood in 1943-4 I had the facilities of the Bass Biological Laboratory through the kindness of Mrs. John Bass. Later the Zoological Research Supply in Sarasota gave me working quarters and Mr. William Hegener helped me to find good collecting places. In 1945 and 1946 the excellent facilities of the Archbold Biological Field Station near Lake Placid were kindly placed at my disposal

by Mr. Richard Archbold, who himself helped me in many ways; there also, my friend and co-worker in botany Mr. Leonard J. Brass, brought me collections of Bidens heads from places that I was not able to visit myself.

THE HOST PLANT

The biological environment of this nomad community is provided and steadily maintained by a single species of plant: the white-rayed subtropical *Bidens pilosa*. This Bidens is a long-lived annual plant that holds its own through the year by producing a succession of long branches. It comes into bloom early. As the first branches mature their fruit and die back, new shoots, arising lower down on the vigorous stock, take their place, and maintain the succession of flowers and fruit. *Bidens pilosa* blooms every day in the year. New flower heads continually developing provide the continuous food supply that a continuing community demands. The Bidens heads contain the richest food products that the plant produces. These foods are concentrated and stored in the seeds for the benefit of the plant's offspring. The insects of this community find these stores, and appropriate what they can of them to their own use.

The heads are of the well-known composite type. From 25 to 50 or more small, yellow, tubular florets stand together in the central position on a flat disc, the receptacle. Each little floret is backed and half-enfolded by a protective scale of its own. At the outer margin of the disc there are normally from five to nine large white florets of another type: strap-shaped and widely outspread, radiating from the top margin of the head, and giving the entire head the aspect of a single large flower. The small disc flowers are fertile, producing single seeds; the large ray flowers are sterile.

Surrounding and tightly enclosing all these flowers, both disc and ray, is an involucre of more or less scale-like bracts in two rows. The bracts of the outer row have green foliaceous tips, that are radiately outspread. Those of the inner row have thin, flat, scale-like tips.

In half-grown flower heads the florets are overtopped and closely covered by the inflexed ends of their own scales; and the whole floret layer, both disc and ray, is covered by the tips of the involucral scales of the inner row, also inflexed, convergent, meeting by their edges, and tightly sealed together. Thus a neat, compact, and altogether sanitary food package is formed in the center of the head. It is the center of attraction for the insects that are hereinafter to be discussed.

There is no way of access to the contained food until the florets by growth and upward pressure have lifted the scales, and opened the door for the insects, so to speak. First of the flowers to open are the white rays. The disc flowers follow, opening progressively from periphery to center; and as the corollas wither the seeds grow up from beneath them with astonishing rapidity. They lengthen and harden and are soon beyond the perils of their infancy.

To this orderly development of the food-store in the young seeds, the insects that would profit by it must conform. Their timing is all-important. They may use the products of the plant only by being on hand and in the proper stage of their own development when the food becomes available.

It is a short period of tenancy that the Bidens head offers seed-eating insects. Few of them can conform to the conditions it sets for them. They must be quick growing, for soft and nourishing foodstuffs in the head quickly dry out and become inedible with the hardening of the seeds. They must be small insects for the food supply in one of these pea-sized heads is very little indeed. They must be equipped in the adult stage with keen senses for finding the heads and with wings for getting to them; and the females have need of an ovipositor for proper placement of their eggs.

THE INSECTS

The animals of this community are nearly all insects. Their degree of dependence as species upon the Bidens heads for food and shelter varies enormously. For present needs they may be grouped in accordance with their place and tenure of residence in or on the heads.

Insects That Live within the Heads

A few important herbivores that are resident within the heads make up the producing class of the community; producers of flesh, that largely sustain the rest of the population. One is a gall maker and the others are green-seed-eaters. Three of the seed eaters are Cyclorrhaphous Diptera, and several are moths. All feed as larvae on the Bidens heads. I begin with the gall-making Cecidomyiid Midge.

Asphondylia bidens Johannsen

This is the species that I found in the first Bidens head split open. It is also the first species that I reared to the adult form, and it proved to be a species new to science. I turned it over to Dr. O. A. Johannsen for naming and he has published a description of it under the above name in the Florida Entomologist for 1945 (28: 9-10).

This species is perhaps the first to gain entrance to the Bidens head after the inflexed covering scales of the involucres begin to lift. The adult is a delicate, long-legged, hairy-winged midge of mosquito-like form, wholly pale brown except for its black eyes, and hardly more than two millimeters in length. The female possesses a long slender ovipositor by means of which she places her eggs singly far down among the corolla buds of an outer row. Possibly, she places the egg within the soft base of a corolla tube. That I have not observed. At any rate the presence of the egg, and of the larva that hatches from it, stimulates the plant to abnormal growth. The base of the corolla expands into a top-shaped gall, several times the normal diameter of the corolla tube. Within this gall the midge passes its larval and pupal stages. The top half of the corolla remains closed as in the bud. The growth

of the ovary (ovule case)into a seed is stopped short, and the plant substance that would normally make a seed is diverted by the presence of the insect to the making of the gall. The walls of the gall thicken and become a deeper green externally, filled with a soft white parenchyma at first that later turns black.

The larva feeds on the soft pabulum that exudes from the surrounding inner surfaces of the gall cavity, and grows with astonishing rapidity. By the time the uninfested corollas of its own row are fully expanded, the larva is full-grown and enters the pupal stage. The pupa is shining, light brown in color, with a double spine on top of the head. It lies loosely within the gall cavity, headed toward the top where it will later make its way out through a hole, and transform, leaving its empty pupal skin sticking half-way out of the hole.

This midge selects for its place of residence the outer florets of a Bidens head. Usually there are several infested florets in a head, sometimes there is excessive infestation, and much crowding, with swelling of the head, and misshapen galls resulting. The greatest number that I have found in a single head is twenty-four; most of them, in that head, aborted by mutual crowding. Ordinarily they are fewer than ten. For example, eight heads taken at Englewood, Florida, on December 24, 1944, had 5, 6, 3, 8, 8, 7, 2, and 9 galls each respectively. When the galls are normally developed the head becomes distended and feels hardened to pressure of the finger tips.

This midge is perhaps the best example I have found of a species in exclusive association with *Bidens pilosa*. It gets into the heads early and develops fast. It does not utterly destroy. Usually at least half the florets of a head are left undamaged by it to produce seeds. It lives and lets live; an example of perfected ecological adjustment. In diverting to gall formation the food supply that the plant is bringing up to its flower heads, the midge accumulates a surplus of nourishing plant tissues, that benefits other insect residents of the heads, as we shall see later.

It is a swift course this insect must run in making the flower its home. Its opportunity is brief. In the bud the flowers are closely covered and inclosed by the overarching bracts of the involucre. After opening, the tissues of the flower quickly mature and harden. The gall must be made and the larva must get its growth between the first exposure of the buds and the end of their flowering.

THREE FLY LARVAE OCCUPY THE CENTER OF THE HEADS

Next in order of importance and in closeness of association with *Bidens pilosa* are three species of little flies that infest the center of the head, and that I have never found in florets of the outer rows. Adults of these flies flit about the opening buds in the sunshine. The females have a long and slender ovipositor by means of which they thrust their eggs deep down among the closely crowded, greenish corolla buds at the middle of the disc.

The larvae of the three appear to feed at first upon the pallid tissues near the base of the corolla and then to turn head downward. They tear to shreds the soft tissues of the developing seeds, and drink in the rich upwelling nourishment in the sap. Their growth in this favored spot is almost as rapid as that of the midge larva within its gall. They feed head-end downward until grown and then they turn about-face and head upwards in proper position for later emergence. The body shortens, the translucent skin slackens and thickens and turns brown; and inside the oblong capsule thus formed, the short pupal stage is entered upon. The three flies are:

1. *Agromyza virens:* Smallest of the three; clear-winged; blackish all over, except for its big red and brown eyes; length about two millimeters.

This species appears to prefer the smaller heads that grow on short lateral branches of the loose flower cluster. The external sign of infestation appears only in older heads in which the faded corollas have fallen from the outer rows of the disc. They leave a patch or tuft persistent in the middle, above the ravaged seeds.

Grown larvae are translucent and rounded on the rear end, with only two little knobs showing darker chitinization. Each of these knobs is the rim of the three-parted spiracle at the outer end of a longitudinal tracheal trunk. After pupation these knobs remain more prominent than in the other two species of flies. The pupal case is smaller and its walls are thinner and of a lighter brown.

Young larvae, that I take to be of this species, tear a hole through the side of the corolla at the level of the lower end of the enclosed anthers, and then enter and feed for a time on the ripe pollen of the flower, before moving down into the seed.

2. *Paroxyna picciola:* This is a larger fly, about $2\frac{1}{2}$ millimeters long; grayish, with shining greenish eyes. The blackish body is thinly clothed with short white hairs and beset with numerous larger black bristles. The wings are gray with many clear spots that become smaller and more or less confluent to rearward. The wing membrane in the clear spots is somewhat irridescent. There is one spot of deep black just before the middle of the wing at the front margin. The female has an extremely long ovipositor that is generally carried sheathed within the long, black, triangular-pyramidal rearmost segment of the abdomen.

The adults flit lightly about among the opening flower in the midst of the tangle of Bidens stems, where they are very inconspicuous indeed. An insect net swept through the weeds, will often take them in considerable numbers where none have been seen. By careful approach and patient watching they may be seen in action; tip-toeing about over the opening heads; lifting their wings and letting them fall. Pairs may be seen in copulation; and females, probing the crevices among the florets with their long telescopic ovipositors.

The larvae of this species appear to do very little feeding in the corollas that they enter. Each goes directly downward into the seed, and eats it hollow,

doing some damage to surrounding scales and to adjacent seeds; at least blackening them. Each one goes head end downward nearly to the bottom of the seed, but generally leaves a stump of it uneaten next to the receptacle. When grown it develops a flat brownish callus that covers its rear end, on which two low button-like triads of spiracles are recognizable. The spiracles are less elevated and less conspicuous than in Agromyza and both larva and puparium are larger. Sometimes there is but one in the center of the head; but oftener there are two, three or even four side by side. As the head dries these become stuck together and may be pulled out in a single tuft along with a crowning tuft of withered corollas.

This species and the next following are members of the well-known fruit fly Family Trypetidae (Trupaneidae). Both immature and adult stages were adequately described and figured by Dr. Foster H. Benjamin in his paper "Descriptions of Some Native Trypetid Flies with Notes on Their Habits" (Technical Bulletin 401, U. S. Dept. of Agriculture, Plates 30 and 31). The wing pattern and venation of both are figured by Curran in his Families and Genera of North America Diptera (1934) and the living colors of the adults are well shown in the plates by Culver in my article in the National Geographic Magazine.

3. *Xanthaciura insecta:* This is the largest of the three species (length about 3½ millmeters) and the prettiest. It is brightly patterned in black and yellow, with coppery eyes that cast green and violet reflections, and with a row of big white spines across the rear of the head.

Its wings are black, with two or three clear dots down the middle and with large triangular notches cut out of the black at both front and rear margins; two notches in front, large and sharply triangular; six or more at the rear, less regular, becoming more or less confluent toward the wing base. The cleared membrane of the wing is brilliantly iridescent. This species is quite as conspicuous as its small size permits it to be; for it prances about over the top of the flower heads in the bright sunshine; displaying its beauties as if with consuming vanity turning its wings this way and that, as a proud lady might toy with her fan.

I found a very minute larva that I took to be of this species, hanging half in and half outside a hole that had apparently just been torn in the side of a corolla near the base. It tears the soft tissues with its paired mouth hooks (which are easily seen at the tapering front end of its body because they are black and all else is white). It sucks the juices of the plant so liberated and feeds downward toward the source of the nourishing saps. It enters the top of the developing seed.

Its growth requires more food than a single Bidens seed will supply. It eats well downward but usually not quite to the bottom of one seed and then laterally into several others before it is grown. Then it turns around to face upward in the cavity of the central seed before pupation. The excess of the fluids liberated in feeding sticks together the unconsumed walls of the seeds; also some of the receptacle scales alongside; and anchors down a number of withered corollas at the top to cap a pupal chamber at the center of the head. The larva is very similar in appearance to that of the preceding species, except for minor details (for which see Benjamin, above cited) that need not concern us here; for it is noticeably larger when grown, of a darker brown or blackish color and has a thicker circular callosity covering the flattened rear end, discoid, and fully as wide as body before it. Moreover, it destroys more seeds, and is generally solitary in the center of the flower head.

MOTH LARVAE INFESTING THE SEED LAYER

Borers are another important ecological group: the larvae of small moths, several species of which are found rather constantly in Bidens heads. These chew their food. They are not restricted to any particular part of the head. They burrow their way through the seed layer, consuming the developing seeds. They are all caterpillars, easily recognizable as such by their shape, by their body setae, by their broad heads and blunt mandibles, by the smooth dorsal shield that covers the first body segment (prothorax), and by the microscopic crochets encircling the tip of their prolegs.

These borers fall in two groups that are strikingly different in size and in pupation habits. The first group includes two genera of very minute moths Phalonia and Lorita. These do not leave the Bidens head until final transformation. Each forms its silk-lined pupation chamber inside a single head. I have found and reared three species of Phalonia, only one of which appears to have been described hitherto: *Phalonia subolivacea.* This species is reported as having been reared from heads of *Bidens pilosa* in Porto Rico.[1]

The other midget moth is *Lorita abnormana*, very similar to Phalonia in size and in general appearance. For lack of precise knowledge of larval characters in this group I was unable to distinguish species among these little borers. What I did observe concerning them, I will set down here, and in a table that follows under the general heading

Phalonias

The work of the Phalonia larvae is recognizable by the presence of silk, which lines their short burrows, holds back frass pellets in the niches, and fastens together withered corollas at the top of the flower head. I have not observed the placement of the eggs or the entrance of the larvae, but I have found the pale larvae of all sizes inside, burrowing irregularly through the seed layer, often in association with the seed-eating flies hereinbefore discussed. When in their progress a larva encounters a fresh green gall it eats that; and when it breaks through the juicy wall of the gall and finds a midge larva or pupa inside, then it eats that. Indeed, it seems to prefer this "prepared" food. Several times I have found a Phalonia larva with its head in a freshly eaten hole in the side of a gall, a half-eaten midge pupa at the farthest

[1] Wolcott, George N., *Insectae Borinquenenses*, p. 483, 1936.

reach of its jaws. Once at Archbold's I found a caterpillar that had cleaned out three galls and was itself inside the walls of the third.

All of which indicates that Phalonia larvae, introduced here as herbivores, belong also among the predators. Indeed, I am not sure which of their two roles is of greater ecological importance. They begin life as seed eaters. I have found what I take to be very young Phalonia larvae eating out the contents of single seeds; and I have also found Bidens heads with well-grown Phalonia larvae in them when no galls were present.

The young larvae are of the typically Lepidopterous form, slender and elongate. When they come upon the richer animal food found in the galls they swell up to almost grub-like form, and grow faster. An acceleration in growth with change to richer food that I once recorded for the larva of the iris weevil *Mononychus vulpeculus* (Biol. Bul. 1: 180, 1900); in that case, however, it was merely an accompaniment of translocation of rich food substances in the normal physiology of the plant.

When fully grown the Phalonia larva extends the silken lining of its burrow upward to form an exit passage, attaching bits of withered corollars to its sides to sustain their walls and to conceal its presence. Within this passage, which serves as a cocoon, the larva transforms to a pupa. I have not determined positively the length of the pupal period, but from freshly gathered heads of Bidens that I put in a rearing jar on the last day of January 1944, Phalonia moths emerged on the 28th and 29th of February. How much of this time was spent before pupation I do not know.

The pupa pushes itself half-way out of a hole at the top, and there the moth emerges leaving its pupal skin in the hole. This skin is about the size of that of the gall midge Asphondylia, but is easily distinguished by the rounded smoothness of the head, and by the presence of two pairs of wings.

The adult moth, a little atom of a Lepidopteron, is nocturnal. After emergence it settles at once with wings and antennae folded closely, on a dry stub or scale or seed, and sits there motionless all day long, perfectly concealed by its camouflage of combined color and form.

The moths of the second group are twice as large as the Phalonias or larger. Their larvae when grown leave the feeding chambers within the heads and find a place of pupation outside. Adults of three genera emerged from heads in my rearing jars: *Mescinia estrella*, *Sparganothis seminolana* and *Palthis asopialis*. The first of these was common; the other two appeared but once each and their larvae I did not see, or at least, did not recognize. I did not know of their presence in the heads when put in the jars.

Mescinia estrella

The larva that I am associating with this moth by reason of equally common occurrence, while other moth larvae of like size were rare, was not reared in isolation. Its identity therefore is not proved; I am assuming it. This larva is easily recognized by the colors of its body. It is brown on the dorsal side marked with four equidistant longitudinal stripes of pale yellow.

A single larva may require more food than the seeds of one head furnish, and may, and probably does shift to a second head, though the actual shifting I have not observed. It eats out all the seeds and finally a big hole in the receptacle beneath them, thus enlarging its burrow. When grown it leaves the head to find a place of pupation outside.

In my rearing jars the larvae crawled actively about exploring the whole interior; sometimes settled down among the loosened seeds and trash in the bottom, but more often they crept about the cloth cover seeking exit. Transferred to a jar of loose trash, they immediately disappaered in it, to reappear some three weeks later as adults again seeking exit.

They do not spin much silk. I have not found anything that I could call a cocoon in the trash after their emergence.

The larvae of this species are not restricted in their diet to Bidens heads. I have reared them also from the heads of a wild sun-flower, *Helianthus cucumerifolius*, and from the heads of the Mexican flame vine, *Senecio confusus*.

Palthis asopialis Guer. This is a rough-scaled blackish moth easily recognized by its huge hind tibiae and by its extremely long palpi. These are curved upward and backward over head and thorax; close-laid when at rest, flung free in action, and densely clothed with long hair-like scales.

The speckled appearance of the wings matches perfectly the salt-and-pepper sand of the Florida coastlands (a mixture of white sand and black humus), and to the soil the moth drops when disturbed. It then scurries to cover like a cricket, darting under the nearest trash and sometimes scattering it about in search of shelter with surprising agility.

Other seed-eating caterpillars are found in the Bidens heads, but are of less frequent occurrence, and the few observations I have made on them are included under their names in the systematic annotated list of the Bidens head population hereinafter presented.

LARVAE OF OTHER HABITS

There are predacious fly larvae to be found resident in the Bidens heads, mostly within the burrows of the herbivores above described. The most important member of this flesh-eating class is a little Tachinid fly (Family Tachinidae).

Lixophaga mediocris Aldrich. The adult fly is blackish, with faint greyish stripings on the back. It is clear-winged like the Agromyza above discussed, but about twice as large. It is easily distinguished from all the adult herbivorous flies of its community by the numerous stout bristles with which its body is beset from end to end.

Adults of this species may sometime be seen flying in the sunshine amid the tangles inflorescense of the Bidens beds, where they are less common than are the herbivorous species. They are more restless too,

make longer flights, and have a peculiar habit of halting in the midst of a flight to weave back and forth laterally at one level, with a shuttle like vibration so swift that the eye can scarcely follow it; then suddenly ending the flight by alighting on a flower stalk, away off at one side.

The larva is another soft white maggot, similar to the larva of Xanthaciura but larger, and it entirely lacks the brown disc like plate on the rear end in that species.

The Lixophaga larva occurs singly in a cavity of the seed layer; presumably the cavity left vacant by the larva that it has eaten. It was present in all localities from which I gathered enough heads for a fair sample, and I have a long series of adult specimens that emerged in my rearing jars. None was reared from larva to adults in isolation. I call it a predator because of the well-known carnivorous habits of the family.

This species occurred sparingly, but regularly, as is befitting a well established predator.

There were a number of other Tachinid flies reared from my Bidens heads, as will appear in the list that follows (p. 444), but this was the only species of that family common enough to be of considerable ecological importance.

An Inquiline. One other very different kind of larva appeared in sufficient numbers and regularity of occurrence to be worthy of special mention here.

Leptodiplosis floridensis Johannsen. This is a member of the family Cecidomyidae (Itoniidae) of gall midges, but it is not a gall maker. Some other species of its genus are predatory in their feeding habits. I made no observations on the habits of this one; it might be a scavenger. It was found in heads from all the localities, but never very common. I have, however, a long series of adult specimens that emerged in my rearing jars.

The midge is perhaps half the size of Asphondylia, even more slender and pale and delicate. It also is pale brown or colorless, and quite patternless, save for several very faint round grey spots in its wings.

The larvae are quite different in superficial appearance from those of Asphondylia; instead of being white and short and fat and arched, they are bright red or pinkish; long, thin and straight. I have always found them in the debris left by other inhabitants of the seed layer of the heads.

Like other Cecidomyiids, this larva has the so-called "breast bone" projecting forward from the front of the first thoracic segment on the midventral line—a little flat sclerotized process with a notched tip.

Chaetopsis fulvifrons. This little Ortalid fly is probably a scavenger, like its close relative *Chaetopsis aenea,* that Dr. W. R. Walton reared in numbers from the abandoned tunnels of the larvae of the moth Nonagria in cattail (Typha) stems (Ent. News, 19: 298, 1910). It appeared sparingly in my rearing jars.

Hippelates pusio, the frit-fly, or eye-fly. This common nuisance of many regions of sand and sunshine is a little clear-winged, blackish midget of a fly that creeps into the corners of the eyes of people, and is not easily brushed aside. It frequents open sunny places out of doors, and is most persistent and annoying on hot sultry afternoons. Its larva is probably a scavenger. The best account of the habits of this fly is that of E. A. Schwarz, found in Insect Life, 7: 374-379, 1894.

Adults of several other species of flies emerged from the heads in my rearing jars; and since their larva must have been living in the heads, unseen, their names are included in the systematic list (p. 444).

INSECTS THAT LIVE IN THE CHINKS OF THE HEADS

Inside the heads of Bidens but outside their tissues there is a little space between the corolla tubes that affords good food and shelter for such insects as are small enough to get in and out of it. It is the space above the seed layer and below the expanded throats of the corollas. Through this space the corolla tubes rise like columns upholding a roof of close-packed yellow petal-lobes. Around these columns run thrips and other very small short-legged insects. All are temporary residents. The smallest of them may live there like migrant families, young and adults together. Others that grow to larger size may live there only in their early infancy.

Thrips. These are the commonest of the insects present, perhaps because they are the smallest. While flowers are fresh some thrips may be found in nearly every head. On splitting a head open they may be seen to run for cover.

They are slender straight-bodied stubby-legged insects, only about a millimeter or two in length when grown. Young and adults commingle, and are very much alike in appearance, except that the adults have wings. The wings are not noticeable at first glance, for they are very narrow, nearly veinless, laid flat along the back of the abdomen, and margined with a long fringe of pale nearly transparent hairs.

Thrips get into the heads as soon as the first florets open. They do most of their damage by gnawing at the bases of the corollas, into the nectariferous tissue. When the last of the florets has opened, the thrips leave for fresher heads. Their minute scarification of the tissues is scarcely noticeable until it turns black. They are so small that their damage to Bidens is of little ecological importance.

I had neither time nor equipment for studying thrips, nor even elementary acquaintance with the group. I merely collected specimens and when my late lamented friend, Dr. J. R. Watson, visited my laboratory in Sarasota in 1945, he named them for me. (See systematic list, p. 445).

Orius pumilio and *O. insidiosus.* These are very small flower bugs (about two mm. long) of the family Anthocoridae. They are small enough and flat enough to slip about, in and out, among the corolla bases under cover. They are very secretive, at least by day. I have taken a few adults in my trap lanterns at night. When driven from one cover, they scurry into

another on their short legs. They are black in color with transparent whitish wing tips.

They appeared sparingly all winter in my rearing jars, and were found in all localities from which Bidens heads were collected in sufficient number to be a fair sample. Nymphs and adults were found in the heads together in January, and pale, newly emerged adults gave evidence that they were in transformation at that time.

They are supposed to be predatory, and to feed on thrips, mites, and other associated insect larvae.

Crevice-haunting only in nymphal stages are a number of species of other families of bugs (Hemiptera) of larger size. Naturally, size always is a limiting factor in fitness for crevice life.

Rhinachlora pallida Reuter. The adults of this plant-bug (Family Miridae) were found on the top of the heads, feeding, mating and ovipositing among the spent corollas at Englewood in February. They are protectively colored. They take flight readily and are diurnal in habit.

Their nymphs are to be found by searching the crevices. As I have not studied them, I can only add the names of those that emerged from heads in my cages to my list on p. 444.

INSECTS FEEDING ON THE OUTSIDE

The outside feeders on Bidens heads are of very great diversity in size and in place and manner of feeding. Some are herbivores, and some are carnivores; some feed by sucking juices and some by chewing tissues; some are adults and some are larvae; some eat ray flowers only and others, the flowers of the disc; but all are transients and not obligate residents in these heads. Only a few of those found most frequently and that are believed to be of some ecological importance can be mentioned here; first a group of beaked insects with sucking mouthparts; and then some larvae with jaws for chewing.

SAP-SUCKING

Stink bugs (Family Pentatomidae) are the largest of the external feeders. Three species are commonly present through the winter season. They are much in evidence because of their size and their habit of clinging awkwardly to the topmost heads. Adults and nymphs are of similar feeding habits. They clamber about over the tops of the heads together. They probe the heads from above with their sucking beaks. Whether sucking the juices of plants or of animals I could not tell; but they seemed to prefer the outer rows of florets to probe in, and they may relish the blood of the gall midge larvae found there.

Thyanta perditor. Adults of this large neotropical Pentatomid were very common (length 9-13 mm.). The leaf-green body is marked by a band of chocolate brown or purplish across its wide front between a pair of laterally projecting, sharp-pointed, prothoracic horns. There is a steeple-shaped spot of the same purplish color on the top of the head. The lateral margins have narrow trimmings of yellow. Pairs of this species were commonly taken on the heads *in copulo* during February. No nymphs were seen in January and February, and only one in December. That one may have been a belated one, left over from the preceding season. Bidens heads seem to be the winter residence for this species and the next one.

Euchistus servus. This is a big grayish, wide-ranging species, slightly larger than the preceding one, quite similar in shape, but its lateral prothoracic horns are less sharply pointed. It is without color pattern. Its back is thickly besprinkled with minute black punctures. Like the preceding species it is very odoriferous. It is less common in occurrence and no nymphs of it were seen on Bidens. In early spring at least it is much more commonly seen on the leaves of orange trees; and in summer, it is a pest of cotton. "After the bolls of cotton form, few are to be found outside of cotton fields."

Sphyracoris obliquus. This smaller (length 7 to 8 mm.) turtle-backed, nearly flightless stink bug seems to be more common on Bidens heads, and more continuously present there in its immature stages. I found nymphs all winter long and in all stages of development (Family Scutellaridae).

Its back is arched like the carapace of a turtle. It lacks prothoracic horns. It is blackish in appearance, with a neat but obscure pattern of paler streaks; one middorsal and a divergent pair on each side. The deep black punctures of its upper surface are more densely crowded than in the preceding species.

The nymphs of this species are somewhat gregarious; perhaps not more so than the laying by the female of many eggs in one place necessitates. They are mostly shining black, rather handsomely marked with yellow. Since all stages (instars) occur together, I infer that the female matures and deposits her clutch over a considerable interval of time.

BROWSING

There are a number of small Lepidopterous larvae (caterpillars) that feed on the tissues of the head from the outside, mainly upon the corollas. The life history of only one of them is known to me; the following one.

Synchlora denticularia. The larva of this species is a "looper" (Family Geometridae). It occurs very commonly on the fading corollas of the Bidens heads, but it is not often seen because of its perfect camouflage. It tears off bits of the brown corollas and attaches them with silk to the tips of the many prominent tubercles that cover its back from end to end. This is the caterpillar shown in Cutler's superb photograph in the article in the National Geographic Magazine (page 353) to which reference has already been made.

The adult is a very pretty delicate green moth that is commonly seen fluttering about lights at night. It has a wing spread of about an inch. It is of a velvety grass-green color above, white beneath, with edgings of pale brick red. Large hemispherical black eyes cover the sides of the head. The plume-like antennae are white-stemmed, and their comb-like fringes are tinged with tan. The palpi are brick red and the

tongue coiled between them is honey yellow. Among the plainer associated moths this one will be easily recognized by its bright colors.

Another Geometrid moth emerged in one of my rearing jars; an undetermined species of *Eupithecia.* It must have been present as a pupa in one of the heads when these were put in the jar. Several additional species of looper larvae were found feeding upon the flower of Bidens, but none of them was reared.

An Unknown Lepidopterous Leaf-tier. There is another moth larva that eats whole heads of Bidens, involucral scales and all. This larva draws the small fresh leaves at the end of the branches close about the developing heads and fastens them together in a bunch with threads of silk. It then feeds inside on both heads and inner leaves. I found a living larva in only one of the leaf-tiers seen, and did not succeed in rearing it.

A little red-rumped lady-bird beetle *(Scymnus haemorrhous)* occurred rather commonly in February and March at Sarasota. It wallowed among the spent corollas of the heads. Like others of its family (Coccinellidae) it is probably a carnivore, and it may have been feeding on the abundant thrips always present with it.

Aphids and Coccids and Their Train

There remain to be considered two groups of outside-feeders that differ much in their way of life from all the others: Aphids and Coccids. They are of great biological interest and ecological importance. Both are viviparous, producing living young. Both are gregarious, forming short-lived colonies. Both are enormously prolific, and capable of quick resurgence after depredations. Both are slow-moving, and defenseless against their predatory enemies. Both secrete honey-dew and are attended by ants that gather it for food. Ecologically both are to be considered by colonies rather than as individuals.

Colony formation proceeds on a parallel with the development of successive branches of the host plant. Infestation of the plant begins when a fertile female flies or drifts in and settles near a growing tip. Her young remain beside her and form a colony; remain until the first settlement becomes overcrowded. Then they spread, going afoot to seek out other growing tips, that on this plant appear in an all-season succession. Wherever they go there goes along with them a regular troupe of predators and parasites, better equipped than they themselves are for travel. We now proceed to consider these two sap-sucking producers of flesh that have so much of biological interest in common, and their very diverse predators.

I begin with the commonest species that I have found on Bidens throughout the winter season.

Aphis coreopsidis. The colonies of this aphid may be found clustered about the growing points of leafy Bidens sprays. They concentrate where the sap is richest, about the base of the flower heads. They spread up over the sides of the head, crowd through the bracts that partly obstruct their passage, and enter any interspaces affording room for them, between the flowers of the disc. Individuals are often seen with beaks inserted in the tissues of the swollen galls; less often, inserted in exposed sides of growing seeds.

Any mature colony will show a few winged female adults, a larger number of wingless females and nymphs of all sizes, frequently some in process of being born. Males are seldom seen.

No aphid colony lasts very long. Its members have no weapons, no armor, no effective repellants. Their enemies feed upon them openly, and only cease feeding when all are gone. The species survives by shifting of place, and quick increase. So many are born that always somewhere a few survive.

New colonies are established when a fertile winged female flies to a suitable fresh location and there deposits an egg. The viviparous female nymph that hatches from that egg becomes the mother of a new colony, herself producing living young almost daily. Her daughters and grand-daughters soon join in to aid and compound the increase. All work together like animated sap-pumps. Each is equipped with a ridiculously long and feeble-looking sucking beak that it manages in some way or other to insert deeply into soft growing tissues. Thus it imbibes sap.

Colonies endure until all are eaten. Destruction by enemies so nearly overtakes increase of individuals that the species survives only by keeping a few jumps ahead—a few successful flights of fertile females to fresh buds.

Aphids were present throughout the winter season and in all places from which I collected Bidens heads except for a short period at the beginning of January 1945, when a light frost (28° F.) occurred. That frost killed nearly all the Bidens plants and quite all the aphids; for a time thereafter I could not find a single colony.

Ants. In a large area of Bidens plants that I had under observation at the time of this frost, ants of several species were common. They were attending the aphids and gathering honey-dew from them. The ants were not killed; but they lost their free ration of honey-dew by this freeze and had to go to work for a living. I found many of them excavating holes into the seed layer from the side of Bidens heads and digging out the soft seeds. Each hole was crowded full of ants, and they fought against removal with the persistence of very hungry animals.

The mealy-bugs *(Pseudococcus citri)* were much less common than aphids on *Bidens pilosa*, and much more local in their distribution. I found them in only a few of the many places where I gathered heads for my rearing jars; but in one of these places—a dump on the bay shore at Englewood—they were abundant. They are always clustered about a few of the terminal joints of flower-bearing branches, their flat bodies closely packed together forming a ring about the stem. The densest ring of them, with the largest number of individuals, always surrounded the base of a flower head. Rarely was an individual mealie found

to have climbed over the rim of the involucre to get in among the flowers.

This uppermost colony I found always attended by a few big, red ants (*Solenopsis* sp.), that were there, collecting honey-dew from the mealies. The ants, trampling roughly over the massed flat bodies, scatter the wax that rises from the glands of their back. The wax rises in columns of snowy whiteness. The columns are broken down also by mealies crawling over each other in search of standing room. When the wax is thus scattered as a whitish powder over their soft pink skins, it gives them an aspect of nudity.

I did not find the mealy bugs in the field until the 28th of April. They were common throughout the month of May, when my opportunity in the field ended.

CAMP-FOLLOWERS

Aphids and mealy bugs are important members of the producing class of the Bidens-head community. They produce the flesh that helps sustain all their camp-followers. These follow the plant's activities from branch to branch, from head to head as these parts successively come into bearing; and these slow-going insects are themselves followed by a train of consumers (predators and parasites) to which we next give consideration. The most important of these predators, generally speaking, are lady bird (Coccinellid) beetles and flowerfly (Syrphidae) larvae.

Coccinellid beetles are predatory in both larval and adult stages. Most of the local species are present as adults through the winter season; the commonest one was *Cycloneda sanguina* (shown in color in Plate IV of Culver's photographs in National Geographic Magazine, Vol. XC, September, 1946).

The adult "lady bird" beetles fly freely about. The females lay their eggs on the under side of opening leaves, singly or in small clusters. Larvae and adults alike enter a colony of aphids or mealies, and feed openly, devouring their helpless victims one by one. When all are eaten in one place, the larvae can generally find another colony by crawling about among the loose branches of the flower cluster; the adult beetles can fly, of course, but they also seem to do most of their food-hunting afoot.

Flower Fly larvae. It is in the larval stage that flower flies (Family Syrphidae) infest the Bidens heads. The species that I found most frequently and observed most carefully is *Baccha clavata.* Its larva grows to large size as compared with aphids. Its growth requires whole colonies, with climbing about in the branch and forks of the flower cluster to find them.

The smallest larvae are found on young shoots bearing immature flower buds, where a few aphids or mealies are already present: incipient colonies. The colors of the Baccha larvae match the pale lilacs and greens of the button-like Bidens buds. Later as they grow larger the larvae become more brightly colored, but hardly more conspicuous. I found them most easily by first looking for their big red ant attendants. The colors are well shown in the plates of my article in the National Geographic Magazine to which reference has been made.

The Baccha larva does not travel caterpillar-fashion, but by another kind of push-and-pull locomotion. It holds for a *push* forward by means of paired fleshy folds (hardly well enough differentiated to be called prolegs) underneath three posterior segments. These folds seem to hold fast to the surface of the plant stem by suction or possibly by simple adhesion. A hold for a *pull* forward is made by means of the extended mouth hooks.

I found a half grown larva wandering on a pedicel that was besprinkled with empty aphid skins, the signs of a devastated colony. I clipped off the pedicel and hung it between two peduncles whose flower buds above the fork were crowded with aphids of all sizes. My larva at once began to climb up one of the peduncles, *sidewise,* releasing and fastening alternately front and rear ends. It soon reached a colony, crowded its way in among the aphids, pushing them aside by lateral swings of its free front end. Having cleared a passage, it set down its extended mouth-hooks for a pull and hauled up the rear end for a new hold. Once set in its customary position, with three fourths of its body enwrapping the twig, it began to swing the free front end with the tip of its mouthhooks extended. It tapped the aphids on the back as if testing them for ripeness, then by a vigorous stroke it drove the hooks deep into the back of one of the aphids, lifted it high aloft, and began to suck its blood. With the compression of the stroke a drop of honey yellow fluid oozed from the tip of each of the two dark green cornicles of the aphid. Its body collapsed. Its empty skin was merely dropped when drained of blood.

When the Baccha larva is full grown it snuggles up under a sheltering Bidens head. Its body shortens to form a kidney-shaped puparium that still half encircles the stem.

With the big, red ants to guide me, I was able to find several dozen pupae, and to rear the adults from some of them, and parasites from others.

All the pupae that I have found have been attached at the underside of spent heads. A single branch, not a single head, is the foraging ground for Baccha when feeding on *Bidens pilosa.*

PARASITES AND SCAVENGERS

These two important and ever present ecological groups have received scant notice in the preceding pages, and are to be dismissed with a mere listing in the pages which follow. I have not studied either. I have only saved the specimens as they emerged from the heads in my rearing jars, and sent them to specialists for naming.

The parasites are a host, and little is known about their ecology. That they are Nature's chief agents for reducing excess in numbers of the non-parasitic species is of course well known. I was surprised to find that I had reared so many species (25) from Bidens heads, and still more surprised that specific names could be attached to so few of them. A num-

ber of species appear to be new to science. They invite a more intensive study by a competent entomological parasitologist.

A few words will tell all that I have been able to find out about the relations between host species and their parasites in the Bidens community. Rearing the residents in the heads collectively by the jar-full is easy, for one has only to take them out as they emerge. But rearing isolated individuals is difficult; first, because it is hard to isolate single specimens without injuring them, and second, it is still more difficult to maintain fit conditions for keeping them alive after their removal from the tight little heads. Evaporation if too dry and moulds if too wet are equally fatal. I spent much time at this, but have to acknowledge getting meager results. However, I succeeded in rearing parasites from isolated specimens of six of the principal herbivores, as follows:

Reared from	Parasites
Asphondylia bidens	*Tetrastichus* sp.?
Xanthaciura insecta	*Halticoptera n. sp.* and *Tetrastichus* 2 species
Paroxyna picciola	*Heteroschema puncta* and *Tetrastichus* 2 species
Agromyza virens	*Callimome* sp.? and *Tetrastichus* sp.?
Mescinia estrella	*Macrocentrus delicatus*
Aphis coreopsidis	*Aphidius testaceipes*

A mass-rearing was made of the parasites of Paroxyna. At a time when these spotwings flies were very abundant and other flies scarce in one particular field, I reared parasites of this fly and determined them by a method of exclusion. Puparia are easily collected, if found when the Bidens heads are shedding their first-ripe marginal seeds. At that time all undamaged seeds are easily loosened from the receptacle, and when removed, there is left standing at the middle of the head a little pencil of agglutinated seed-remnants and scales. Each pencil tightly surrounds one or more puparia. I gathered a lot of these pencils (perhaps 100 of them) while the collecting was good, put them in a rearing jar and waited to see what adults of both flies and parasites emerged.

The yield was gratifying; perhaps half a hundred Paroxynas and no other flies at all. Parasites of seven species, some of which were doubtless hyperparasites. Arranged in the order of numbers present and beginning with the most numerous the parasites were: *Tetrastichus* two species, *Heteroschema punctata, Halticoptera* two *n. sp., Habrocytus sp.?, Eupelmus sp.?, Zyglyptonotus schwarzi, Horismus sp.?.*

The Scavengers of the community are fewer, and little is known about their operations. In the small heads of Bidens there is not much of a clean-up job to be done, for the seeds and their enveloping scales fall away early and completely.

THE BIDENS COMMUNITY

Thus far we have been considering species in their individual ecological relations. Now I wish to present some data on the Bidens Community as a whole. I begin with the producing class, the herbivores; the class that directly or indirectly provides food for all the other classes. I select six species as the chief representatives of that class and present in Table 1 my record of their occurrence in sample collections they were made in ten different localities spaced well apart over the lower third of peninsular Florida.

TABLE 1. Seed-eating larvae from 100 heads of *Bidens* pilosa.

Date	Gall Midge	Flies			Moths		Source of Collection
		Band wing	Spot wing	Clear wing	Phalonias	Mescinias	
19 XII 1945	142	1	5	11	2	1	De Soto City
25 XII 1945	17	1	2	15	2	1	Archbold's, Lake Placid
30 XII 1945	5	3	21	1	3	0	Delray
14 I 1946	44	3	3	3	0	2	Park Avenue, Sarasota
30 I 1946	34	3	7	4	5	0	Jungle Gardens, Sarasota
12 II 1946	10	1	4	1	8	0	Davis Island, Tampa
19 II 1946	4	2	6	3	3	3	Woodmere
23 II 1946	10	2	2	5	5	1	Terra Ceia, Island
26 II 1946	8	2	9	17	6	1	Ochopee
16 III 1946	31	2	2	1	3	0	Bradenton

(1) Gall midge, *Asphondylia bidens*.
(2) Band wing fly, *Xanthaciura insecta*.
(3) Spot wing fly, *Paroxyna picciola*.
(4) Clear wing fly, *Agromyza virens*.
(5) Phalonias; small moths that pupate in the heads.
(6) Mescinias; larger moths that pupate outside.

The samples were small, but unselected, save that uninfested heads (which rarely were found) were not included. The counts were made by dissecting heads and sorting their insect residents.

My rearing jars yielded many additional species, but no others (save only diminutive thrips, mites and parasites) were so constantly present. The localities ranged well over south peninsular Florida, the first two of the table being from the south end of the central ridge in the Florida scrub, the third from the East Coast, the others from the West Coast excepting Ochopee, which is deep in the Everglades. Localities offered no significant differences. A glance at the table will show that by dissecting the infested heads from anywhere in this region, one might expect to find all these herbivorous permanent residents.

It should be noted that these six species fall into three ecological segregates based on their ways of living; three economic patterns, so to speak:

(1) The midge spends both larval and pupal stages in the gall which feeds it.

(2) The fly larva, having no jaws, but only mouth hooks, tears the soft seeds to shreds and sucks the liberated fluid contents of the seeds.

(3) The moth larva devours the seeds bodily, and ranges more freely.

The table shows that although some species were absent betimes, each of the three ways of picking up a livelihood was present in all the localities.

These herbivores were accompanied by other less constant residents in the heads; thrips and parasites were generally present, and mites also, less frequently.

I had neither time nor equipment for the study of these.

The predatory larva of *Lixophaga* was present often and many others, that are named in preceding pages, less frequently.

Fluctuations in numbers of individual of a species were frequently noticed, but not studied. The 142 specimens of galls in the 10 heads from De Soto City (first line of the table) was an example of a "high" near its peak for that species. There was a heavy production of galls in December, 1945, at Englewood, followed by a speedy decline in January, where gall midge parasites swarmed for a time. Then the parasites, having largely destroyed their own food supply, dwindled in February. Such waves of upsurge and decline are, of course, well known to economic entomologists.

Casualties befall the Bidens community destroying the host plant together with insects that are dependent on it for food; in this region, mainly fires and frosts. Agricultural operations are hardly to be ranked as casualties on Bidens; for while tillage destroys, it at the same time opens for settlement new untilled areas, where the vagrant Bidens seeds quickly enter and take possession for a time.

Such is the complexity of the web of life that a casualty to one species may be a benefit to another. Following the January 1st frost just mentioned, some frost-bitten heads got into one of my jars. From that jar there emerged a larger number of psocids *(Coecilius croesus)*. They may have come from eggs laid on the matted and fermenting corollas. The species is probably to be ranked as a scavenger.

A better idea of the normal resident population of the heads will be gained if I set down the rearings from four single collections of heads made in the months of December, January, February and March of 1943-4 at Englewood. For each catch more than 100 heads were clipped off, cleared of spiders, ambush bugs, aphids, and other outsiders, and put in four rearing jars, and kept there until no more emergences of adults occurred. Thrips, mites and parasites were not counted. These aside, the combined totals for all four jars were as follows:

Asphondylia bidens ...	52	*Lixophaga mediocris* ..	2
Xanthaciura insecta ...	23	*Mescinia estrella*	4
Paroxyna picciola	.130	*Leptodiplosis floridanus*	16
Agromyza virens	19	*Orius pumilio*	5
Phalonia spp.	26	*Scymnus haemorrhous* ..	2

A Bidens Community in Action. Once I saw Bidens and its train taking possession of new territory. Fortunately it was a block of land not far from my own abode in Sarasota, and I could visit it often and see what was going on. The block was "hammock" land adjacent to the Jungle Gardens. The entire block had been for years so heavily shaded by trees, big and little, that there were no green herbs growing on its soil, save on the extreme edges along bordering roads. In December 1945 it had been cleared of all trees and brush, and "opened for settlement," so to speak. It lay fallow. Bidens seeds were waiting. They "got in on the ground floor" and almost covered it during late winter and early spring with freshly blooming clumps of flowers.

I made me a one-legged stool, and set it down among the flowers near the center of the block and sat for repeated hours in the sunshine, trying to see what I could of the Bidens community in action. As was to be expected, the best flyers had arrived first, along with many bees and butterflies. Spot-wing flies (Paroxyna) were abundant, but there were no gall midges *(Asphondylia)*, no aphids, no moth larvae in the heads at first, though they came in plenty later. A Tachinid fly was seen on the wing; the frail inquiline midge, *Leptodiplosis*, arrived much later. Of feeders on the outside of Bidens, I saw many green stink bugs *(Thyanta)*, but the near-flightless turtle-back had not yet arrived. I saw one Scymnus beetle half buried among the fading corollas of the disc.

All adult members of the colony were very active in the hours of sunshine. The abundant Paroxynas were running up and down the long smooth internodes of the branches of the flower cluster, or were inspecting the tops of the flower heads. A much shyer *Lixophaga* could be seen betimes, darting into view and out again; occasionally pausing in mid air to hover momentarily in the dizzy manner already herein described. A few black thrips were flying. Parasites of Paroxyna and of other fruit-flies of the genus *Halticoptera* were also abundant. Their flight singularly resembles that of *Lixophaga*, but is less swift; the same shuttle-like weaving back and forth in mid-air, with sudden disappearance afterward. To the unaided eye these parasites appear to be mere black specks in air or on green leaf; but they are easily taken, even in flight, on the tip of a wet feather dipped in alcohol.

I used a sweeping net to take a sample of the things flying among the Bidens flowers; a small net that I could swish in and out among the branches of the open panicles. The meshes of the net (No. 000 silk bolting-cloth) were too wide to retain the parasites. The catch of larger forms was:

4 Band-wing flies	1 Lixophaga
45 Spot-wing flies	3 Green stink-bugs
16 Clear-wing flies	2 Green plant-bugs
1 Phalonia moth	Several scatterlings

The nectar of the flowers attracts a host of insect visitors, ranging in size from swallow-tail butterflies and oleander moths downward. Of these I am taking no account in this paper.

These notes of mine are fragmentary. They cover observations made, as opportunity came, in the winter season and early spring. I offer them now because there is little likelihood that I myself shall be able to extend them. And I suggest that perhaps a more prolonged and more intensive study of the Bidens community, with careful census-taking and experimentation might bring new and useful knowledge of the principles of animal communities in general; principles that possibly operate in human communities as well. The shifts of population and the com-

mingling of participants occur so quickly that one may witness many repetitions of them in a short time.

ANNOTATED SYSTEMATIC LIST

Having now reviewed briefly the members of the community that seem to be of most ecological interest, I will add a list of all the insects that I have found living within the heads of *Bidens pilosa* or feeding upon them externally, save only flower visitors. Were I to include those that come only to feed on nectar and pollen, my list would probably be nearly doubled. Charles Robertson listed 133 species of insects as visitors to the yellow-flowered *Bidens aristosa* of the Mississippi Valley (Robertson, *Flowers and Insects*, page 58. Carlinville, Illinois, 1928).

Species severally discussed in the preceding pages are marked with an asterisk *. After the name of each species or group of species, I have placed the initials of the determiner. Family names in parentheses follow.

At the end of this study I find myself indebted to twenty-six systematic entomologists for determination of the names of the species herein discussed; most of all to my Cornell colleagues on whom I have made repeated demands: Doctors Henry Dietrich, O. A. Johannsen, W. T. M. Forbes, and J. C. Bradley; and to Mr. C. F. W. Muesebeck and his Staff of the Division of Identification of the U. S. Department of Agriculture. The list is long and the names of the 26 in alphabetic order are: Bottimer, L. J., Bradley, J. C., Buchanan, L. L., Busck, August, Dietrich, Henry, Forbes, W. T. M., Gahan, A. B., Greene, C. T., Heinrich, Carl, Huckett, H. C., Johannsen, O. A., Knight, H. H., Lambert, Robert, Leonard, M. D., Morrison, Harold, Muesebeck, C. F. W., Nunenmacher, F. W., Readio, P. A., Reinhard, H. J., Rehn, James A. G., Steyskal, George, Stone, Alan, Tissot, A. N., Townes, H. K., Watson, J. R., Weld, L. H.

ORDER DIPTERA

**Asphondylia bidens* Joh. O.A.J. (Cecidomyiidae) Gall maker

**Leptodiplosis floridanus* Joh. O.A.J. (Cecidomyiidae) Predator or scavenger?

**Agromyza virens* Loew. C.T.G. (Agromyzidae[1]) Seed eater

**Paroxyna picciola* Bigot. G.S. (Tephritidae) Seed eater

**Xanthaciura insecta* Loew. G.S. (Tephritidae) Seed eater

**Lixophaga mediocris* Townsend. H.J.R. (Tachinidae) Larval predator

Sarcophaga occidua Fabr. H.J.R. (Tachinidae) Larval predator

Sarcophaga rapax Wlk. H.J.R. (Tachinidae) Terra Ceia Feb. 24th 1946

[1] *Agromyza pusilla* is recorded by Wolcott as having been reared from heads of *B. pilosa* in Puerto Rico. (*Insectae Borinquenenses*, p. 383, 1936.)

Cochliomyia macellaria Fabr. H.J.R. (Tachinidae) Sarasota Jan. 3d 1946

Gonia sequax Will. H.J.R. (Tachinidae) Sarasota Jan. 3d 1946

Archytas piliventris v.d.W. H.J.R. (Tachinidae) Feb. 1st 1946

**Hippelates pusio* Loew. O.A.J. (Chloropidae)

**Chaetopsis fulvifrons* Macq. O.A.J. (Ortalidae) (Muscidae) A pictured-wing fly

Lispe albitarsis Stein. H.C.H. (Anthomyiidae)

Taeniaptera lasciva Fabr. G.S. (Trixoscelidae) Ochopee March 7th 1946

Spilochroa ornata Johnson. G.S. (Lauxanidae) Feb. 13th 1946

Neogriphoneura sordida Wied. G.S. (Tetanoceridae) Feb. 1st 1946

Minettia punctifer Mall. G.S. (Tetanoceridae) Feb. 1st 1946

Caliope lutea Coq. (Tetanoceridae) Feb. 13th 1946

Dictya sp.? G.S. (Tetanoceridae) March 2nd 1946 Sarasota

Ceratobarys eulophus Loew. G.S. (Milichiidae) Feb. 12th 1946

Pholemyia sp.n. G.S. (Milichiidae) Feb. 13th 1946

**Baccha clavata* Fabr. O.A.J. (Syrphidae) Abundant in early spring

LEPIDOPTERA

**Phalonia subolivacea* Wlsm. W.T.M.F. (Phaloniidae) Common

Phalonia two n.sp. W.T.M.F. (Phaloniidae)

Lorita abornana Busck. W.T.M.F. (Phaloniidae)

**Synchlora denticularia* Walker W.T.M.F. (Geometridae) Feeds on corollas of disc flowers

Eupithecia sp.? W.T.M.F. (Geometridae)

**Palthis asopialis* Guen. W.T.M.F. (Noctuidae)

**Mescinia estrella* B. & McD. A.B. (Pyralidae) Common

Sparganothis distincta Wlsm. R.L. (Tortricidae) Adults common at lights

Sparganothis rostrana Walk. R.L. (Tortricidae) Reared at Archbolds Jan. 14th 1946

The last two are broad-shouldered reddish brown species.

HEMIPTERA

**Thyanta perditor* Fabr. P.A.R. Green stinkbug (Pentatomidae)

A neotropical species near its northern distribution limits; apparently not breeding in December and January. Common.

**Euchistus servus* (Say) P.A.R. Gray stinkbug. (Pentatomidae)

A wide ranging species; Mass. to Calif. and southward. A cotton pest in Texas, common there

after April 1st. "After the bolls form, few are found outside the cotton fields." Very common about Sarasota in March and April.

**Sphyrocoris obliquus* (Germ.) P.A.R. Turtle-backed stinkbug (Scutelleridae)

Another neotropical species found breeding through the winter months. Common. Observed only on the heads of *Bidens pilosa.*

Leptoglossus phyllopus (L.) P.A.R. (Coreidae)

A large predacious species (length 18-20 mm.) found on Bidens heads only at Turner River in the Everglades; long-legged, brown in color with white crossband on the back and with leaf-like expansion of the hind tibia. Scatterling.

Sinea diadema (Fabr.) P.A.R. (Reduviidae)

A smaller predacious species (length 12-14 mm.), of wide distribution U. S.; common also on flowers of other Compositae; heretofore reported as a predator on aphids.

**Harmostes affinis* Dallas and *H. serratus* (Fabr.) P.A.R. (Coreidae)

Pale plant bugs smaller (length 6 or 7 mm.). Nymphs of all stages and adults very common on and in the heads of Bidens at Englewood in Jan. and Feb. 1944.

**Rhinachloa pallida* Reuter. H.H.K., and 9. *R. subpallicornis.* P.A.R. (Miridae)

Both emerged from Bidens heads in February at Sarasota and at Englewood in 1944.

Lygus apicalis (Fieb.) P.A.R. (Miridae)

A cosmopolitan species; a common scatterling on Bidens heads; very small (length about 5 mm.), the color ranging with age from pale translucent green to brick red. Sarasota in March.

Nysius californicus Stal, and *Belonochilus koreshanus* V.D.; both P.A.R. (Lygaeidae)

The former said to hibernate in Spanish moss, was reared from Bidens heads at Sarasota on Feb. 17th 1946; the latter, species said by Van Duzee to abound in the heads of Florida Pennyroyal *(Pycnothymus rigidus)*, young and adults together. Emerged but once in a rearing jar on Feb. 7th at Sarasota.

**Orius pumilio* Champ., and 14. *O. insidiosus* Say H.H.K. (Anthocoridae)

Both minute flower bugs. Common in the heads throughout the winter at all stations.

Aphids

**Aphis coreopsides* Thomas A.N.T. The commonest aphid.

Aphis spiraecola Patch M.D.L.

Mealy bugs

**Pseudococcus citri* (Risso) H.M.

COLEOPTERA

Epicauta strigosa Gyll. H.D. (Meloidae)

Epicauta lemniscata Fabr. H.D. (Meloidae)

Macrobasis tenuis Horn H.D. (Meloidae)

Diachus auratus Fabr. H.D. (Chrysomelidae)

Melanopthalma picta, Lec., and *M. distinguenda* Com. H.D. (Lathrididae) Scavengers?

Cathartus rectus Lec. H.D. (Cucujidae)

**Limnobaris concinnus* Lec., and *Derelomus basalis* Lec. H.D. (Curculionidae)

Phyllobora 20-maculata Say F.W.N. (Coccinellidae) A lady-bird

**Coccinella sanguinea* L. F.W.N. (Coccinellidae) The commonest lady-bird

**Scymnus haemorrhous* Lec. F.W.N. (Coccinellidae)

Acanthoscelides ochraceicolor Pic. L.J.B. (Bruchidae)

Sennius sp.? L.J.B. (Bruchidae) Seed-eater

Cathartus quadricollis Guer. Reared twice. "Often found in cotton bolls."

PHYSOPODA Thrips

Frankliniella aphalica J.R.W. A pale yellow species, everywhere common.

Haplothrips gowdyi J.R.W. A slightly larger black species, only a little less common.

Thrips abdominalis J.R.W. A red-and-black-banded species; least common.

CORRODENTIA

**Caecilius croesus* Chapman. J.G.N. Emerged several times in my rearing jars, always in considerable numbers, and from jars in which there had been some growth of molds, and only from jars containg heads that had been nipped by frost before they were collected. Scavengers?

ORTHOPTERA

Aptenopedes sphenariodes Scudder J.A.G.R.

This is a beautifully colored wingless species, its back leaf green, its sides deep violet. It feeds on the ray flowers of Bidens. One was seen to devour the blades of four fully expanded rayflowers in rapid succession, leaving a rayless disc.

**Scudderia* or *Inscudderia* sp.? J.A.G.R.

Newly hatched nymphs of this katy-did were collected a number of times from full-blown heads of Bidens. They were not observed feeding; perhaps the heads furnish them only a nursery for incubation of the egg.

HYMENOPTERA

CHALCIDOIDEA A.B.G.

**Callimome anthomyiae* Ashmead. Reared on January 7th 1946 from heads collected at Delray. Common.

Callimome "sp." Sarasota, January 7th 1946. Common.

Habrocytus "sp.?" Reared in numbers from heads collected at Sarasota in March 1946.

**Halticoptera "n.sp."* Reared from puparia of *Xanthaciura insecta* at Archbold's, December 14, 1945; also from puparia of *Paroxyna picciola* at Sarasota in March 1946; generally common.[2]

**Heteroschema punctata* (Ashmead). Reared in num-

[2] *Halticoptera aenea* is reported from *B. pilosa* in Puerto Rico: "Insectae borinquenenses," p. 534.

bers from my pure culture of *Paroxyna picciola* at Sarasota in March 1946. Constantly appearing in my rearing jars.

Horismenus "*sp.?*" From heads collected at Delray December 30th 1945.

Rileya "*sp.n.*" From heads collected at Delray December 30, 1945.

Spilochalcis flavopicta (Cresson). Emerged from heads collected at Tampa on the 22nd of February 1946. A grotesque creature indeed.

**Tetrastichus* "at least two species." Reared from puparia of *Agromyza virens* at Sarasota on March 1st 1946.

Torymus "*sp.*" Emerged at Sarasota February 12th and 18th 1946. Reared from *Paroxyna picciola* at Sarasota in March 1946.

Zaglyptonotus schwarzi (Crawford). From heads collected at Sarasota in March 1946.

BRACONIDAE C.F.W.M.

—An undetermined genus of Microgasteridae: 3 males from heads that were collected at Tampa February 22nd 1946.

Apanteles "apparently undescribed." Emerged from heads collected at Delray on December 30th 1945.

Aphidius (Lysiphlebus) testeipes (Cresson). Reared from *Aphis coreopsidis* heads collected at Delray on December 30th 1945.

Brachymeria incerta Cresson. Emerged from heads collected at Englewood on January 5th 1944.

Bassus buttricki (Viereck). A single specimen emerged at Sarasota December 12th 1946.

Ceraphron "*sp.?*" Emerged at Sarasota March 16th 1946.

Chelonus "*sp.?*" "Probably undescribed" from heads collected at Sarasota on March 16th 1946.

**Macrocentrus delicatus* Cresson. This large pale Braconid is a well-known parasite of small Lepidopterous larvae of several families. It is too large and too common to have developed in any other species that I reared from Bidens heads except *Mescinia estrella;* other moths large enough to be its host appeared far too sparingly in the jars to supply the long series of specimens of *M. delicatus* that I reared.

Microbracon gelechiae (Ashmead). Emerged from heads collected at Sarasota February 28th and again on April 12th 1946.

Pachyneuron allograpta Ashmead. Sarasota January 14th 1946.

Phanerentoma "*sp.*" Emerged at Sarasota February 2nd and February 28th 1946.

Rogas "*sp.?*" Emerged at Sarasota March 2nd 1946.

HYMENOPTERA

ICHNEUMONIDAE H.K.T.

Pristomera euryptychiae Ashmead. A single specimen emerged on March 1st 1946 at Sarasota. Dr. Townes remarked concerning it: "A parasite of small caterpillars."

CYNIPOIDEA L.H.W.

Trybliographa "*sp.*" Emerged in small numbers on February 18th and 20th 1946 from heads collected in Tampa on Davis Island. Dr. Weld remarked concerning it: "A parasite of Diptera."

SUMMARY

The common wayside weed, *Bidens pilosa*, by reason of the manner of its growth, is able to maintain year-long production of flowers and fruit. Its heads of flowers provide food and shelter for a nomad community of small insects. I call it a community because its resident members are producers and consumers, parasites and scavengers, continuously performing the necessary functions that fall to these classes in every animal community.

While each species minds its own business, each has a share in the established order of the community, and each has its troubles in maintaining that share: troubles with predators and parasites and competitors; and all members together are beset by casualties that overwhelm. Generations succeed each other with the rapidity of the blossoming and ripening of the heads.

The members of the producing class (producers of flesh) are here as elsewhere, most numerous, and most constantly in residence. One midge larva *(Asphondylia bidens)* causes galls to grow in many outer corollas. The larva of three species of flies feed on the fluid contents of any seeds at the center of the head. The larvae of several moths eat their way at random through the developing seed layer of the head. A predatory tachinid larva pursues some or all the above herbivorous larvae through their tunnels in the seed layer.

It is only in the larval stage that insects get inside the tissues of Bidens to feed. A few adults are small enough to live in the chinks between the corollas of the head. A greater number of mostly larger species feed openly upon the outside.

The predatory members of the community are mostly larger and more widely ranging species, that are mainly transient residents or scatterlings. They feed from the outside, some on blood, some on flesh, and few of them have lifelong association with Bidens heads in both larval and adult stages.

The parasites are a host, and little is known as yet about their ecology; but it is well known that they are collectively nature's chief agency for reducing overpopulation of the other members of non-parasitic species. Hyperparasites in like manner serve to control excess of primary parasites.

The scavengers are fewer and small and very little is known about their operations. In the small heads of Bidens there is not much of a clean-up job to be done.

This *Bidens pilosa* in its own limited way, provides its insect tenants with all that the best of communities can offer: food and shelter and fit conditions for the nurture of their young.